THE AMERICAN
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THE AMERICAN NATURALIST is a bimonthly journal devoted to furthering the objectives of The American Society of Naturalists which are the "discussion, advancement and diffusion of knowledge concerning the broader biological problems, including organic evolution, thus serving to correlate the various biological sciences into a common philosophy of biology." It will publish those general addresses, essays and papers presented at the symposia of biological societies which contribute to the above purpose; research papers and reviews in which theoretical interpretation and synthesis are predominant; and brief discussion, criticism and comment on material published in this journal and elsewhere. "Letters to the Editors" containing new information or comment will be dated when received and published in the next issue. They should not exceed two printed pages.

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THE PLACE OF ECOLOGY IN SCIENCE*

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This joint session of the American Society of Naturalists and the Ecological Society of America represents the 77th meeting of the American Society of Naturalists, founded in 1883. I have the honor of giving the 75th presidential address—an uneasy one as I contemplate the titles of those given by my distinguished predecessors. I am again reminded, as I was on a somewhat similar occasion, of a bit of doggerel apropos of an early president of the Royal Society of London:

> "And when he woke and found himself in Newton's chair
> He wondered how the devil he got there."

Yet I am not wholly without comfort. If it has not been my privilege to engineer any of the dazzling advances in biological science of recent decades, I assume that my efforts to interpret some of them to laymen have been appreciated. It was, in fact, the shock, nearly thirty years ago, at discovering the serious social consequences due to public ignorance of basic ecological principles, that diverted me from interesting technical studies. Even so, this experience has been professionally rewarding, for it has obliged me to give considerable thought to principles, and enabled me to effect some synthesis of social and biological science. It has also led me to a staunch belief in the importance of the naturalist as such (Sears, 1944).

The first call (1883) for the organization of the American Society of Naturalists as reprinted in the Records of the Society (Amer. Nat. 93, suppl.) is instructive and worth quoting here.

"A number of American workers in Biology, desiring to have established an association of American naturalists for business purposes, extend to you a cordial invitation to join in a movement looking toward that end.

"The intention is to have an annual meeting, for the purpose of discussing topics of common interest, for which, at present, no opportunity

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*Address of the President, American Society of Naturalists, delivered at the symposium on Interactions in Nature, cosponsored by the Ecological Society of America and the American Society of Limnology and Oceanography at the meeting of the American Association for the Advancement of Science, Chicago, Illinois, December 27, 1959.

is afforded; as, for example, museum interests, in connection with which each museum director could indicate his plan of work, the special group of which he was making exhaustive collections, so that work may not be uselessly duplicated in many places; methods of museum work; methods of exhibition etc.; methods of laboratory work; laboratory technique; new and valuable points in staining, mounting, cutting, and preserving of sections; systems of instruction in various departments of natural science; methods with small elective classes; with large college classes; the position which the observational sciences should hold in the college curriculum; the amount of natural science which should appear in college entrance examinations; the amount and character of such instruction in preparatory school, etc.

"It is further believed that such a society could materially influence for the better the cause of science in America; that it would have a very healthful general effect, and could exert a strong influence in many directions where at present it seems to be very much needed."

While the organizing group was concerned frankly with what it called "business"—means rather than ends—the end seems clear enough from the subsequent record. At the time, and for a generation thereafter, evolution was the guiding concern of most naturalists. They were occupied largely with the search for further evidence of it, and for applying the theory to an interpretation of the organic world. It infused, as it still does, their elementary teaching, based on the sequence of evolutionary types.

Thus when the rediscovery of Mendelism came at the turn of the century, the Society was a logical and effective instrument for sponsoring the study of variation and inheritance. As such it has been the virtual foster-mother of American genetics, and even since this infant science has become a husky adult, safely launched and preeminent throughout the world, a substantial portion of symposia and presidential addresses have been devoted to it.

This being the centennial year of the *Origin of Species*, it is appropriate to remind ourselves that in it Darwin presented the germs of two new sciences. He did not christen either of them, but he did have this to say:

"A grand and hitherto untrodden field of inquiry will be opened, on the causes and laws of variation, on correlation, on the effects of use and disuse, on the direct action of external conditions, and so forth."

To a remarkable degree the American Society of Naturalists has aided in the brilliant fulfillment of this prophecy so far as genetics is concerned.

The other science was ecology, so named a decade later by Haeckel. It was not only implicit in, but exemplified by the *Origin*. Robert C. Stauffer who has had access to unpublished material reports (*Science* 130: 1449-1452, 1959) that without abridgement Darwin's *Origin* would have been even more definitely and explicitly an ecological treatise. Yet I do not recall ever seeing this work referred to as basically an ecological study. It is precisely that, for its whole thesis concerns the interaction of life and en-

vironment, oversimplified though it was in Darwin's phrase "the direct ac-
tion of external conditions." Significant, too, is the fact that while his book
links what we now call genetics with ecology, this essential relationship
was long neglected thereafter, until its importance was reasserted in such
work as that of Turesson, Clausen and Keck, Olmsted, MacMillan, Cain and
others. The very term ecology lay dormant from 1869 until its revival by
Warming in 1895. Its identification entailed a vast amount of concentration
on the structure, composition and development of communities, as well as
on the adaptive features of animals and plants.

During the incubation period of modern genetics any attention that plant
ecologists, then laying a foundation for their science, gave to variation was
concentrated on the remarkable plasticity of form and physiological response
to be found in plants. Not surprisingly, these striking phenomena in some
cases lowered the bars of caution which were at the same time being erected
by the geneticists. I can still recall my own impressions when, fresh from
the study of Castle's pioneer text in animal genetics, I began to learn of the
effects of light and moisture on plant form. I must confess that it took some
thought and experience, even after hearing Johannsen's lectures in 1912, to
be properly skeptical about the heritability of environmentally induced
variations.

I have elsewhere discussed some of the early vicissitudes of ecology and
its exponents, especially in the United States (Sears, 1956). To a degree
some of these handicaps still persist, but since minds, like water, eventually
find their level even in the sluggish stream of academic conservatism, I am
concerned only with the status of ecology as it affects the intellectual and
material welfare of the nation. On this last point I can speak from ex-
perience.

I have recently heard ecology described as a kind of intellectual halfway
house, whose justification will disappear when physiology has been reduced
to proper mathematical precision. I feel no particular urge to combat this
suggestion otherwise than to remark that halfway houses exist because of
their usefulness on the way up and that their occupants are not necessarily
half-wits.

Scientists distinguish their methodical approach from crude trial and error
by calling the latter empirical. Philosophers, taking advantage of their ir-
ritating freedom on the side lines, recognize correctly enough that science
itself is a matter of trial and error, however refined. To them, scientific
knowledge is also empirical—a wholesome thing for us to keep in mind.

This means that the scientist has both right and duty to tackle phenomena
at any level that interests him, whether it is millions of light years away or
under his feet. X and Y are powerful tools, not likely to be replaced by any
degree of cleverness in handling Arabic numerals. On the contrary, they are
necessary to set the stage for proper calculations.

The world of knowledge would be infinitely poorer if it were unlawful to
study an animal until we had a complete dossier of its intermediate metabo-
lism and biochemical genetics. More than that, it is our knowledge of the

organism as a whole that gives point and meaning to more detailed and pre-
cise analysis.   Any tendency to construct a hierarchy of scientific values
in inverse proportion to a scale of possible precision should be scotched,
not as a matter of personal privilege, but on the score of plain intellectual
honesty.

The physicists are now working with brilliant results on the ultimate com-
ponents of matter.   But they would be the last to assert that they are near
the end of the road, or that the study of higher levels of organization is de-
modé, unprofitable or essentially of less scientific importance than the tasks
that engage them.   Their camp-followers, as is so often the case, are per-
haps less perceptive.

Granting fully the need to analyze the components of any system, the sys-
tem itself, and systems of systems are no less important to understand. How
else are we to justify the study, by radiotelescopy, of galaxies innumerable
light-years removed, far beyond the reach of visual inspection? Shall we
postpone or depreciate the scientific merit of this costly enterprise simply
because we have so much to learn of phenomena closer at hand and of lesser
scale? (I speak only of scientific merit, not economic priority.) In truth,
studies at both ends of the scale of magnitude are mutually complementary,
as necessary to each other as cell to body and body to cell.

Analysis is the instrument of perspective, and sound perspective the end
toward which science serves the human mind.   Perspective becomes mani-
fest to us in form, organization and process.   Only as these are understood
do the results of analysis become significant.   Only as analysis proceeds
does it provide knowledge and techniques for the study of large and complex
phenomena. One of the most disturbing trends in modern biology is the tend-
ency to undervalue the classical aspects of that subject.   Doctoral candi-
dates have been known to report learnedly on minute characteristics of or-
ganisms of whose taxonomy—to say nothing of their relationships in the liv-
ing state—they knew little or nothing. While this may be explained by the
exacting demands of critical modern techniques, it cannot be excused so
readily.

Scientists being human, they are naturally drawn to activities that are at
the moment exciting.   Yet I believe it can be shown that the great advances
(now referred to as break-throughs) have come from re-examination and ques-
tioning of situations that seemed commonplace and self-evident.   Men had,
for millenia, seen with their own eyes burning logs transformed into gas,
liquid, solid and light: air, water, earth and fire.   What more obvious than to
classify fire as a fourth element and the gases as unknowable because in-
visible?   Modern physical science was born when these assumptions were
questioned, but only because the original analysis of the general pattern of
combustion was at hand.   Modern man sees fire as his ancestors did, but
with a richer appreciation.   A mathematician friend sitting before our fire-
place once remarked "I cannot have a hearth in my house. If I did I would
never get any work done. I would be watching the fire instead."

Unless I completely misunderstand the function of higher mathematics,
much of it has been developed to enable us to express relationships among

complex systems which we may not, for the time being, be able to analyze in detail. Were it otherwise, of what use would be the italic f, the function sign, symbol of analysis deferred? The invention of new techniques and instrumentation for refined study of detail does not make older, more general knowledge obsolete and superfluous. Instead, it is our clear understanding of the general which stimulates and gives point to refinements. In identally, the quality of effort, intellectual and manipulative, required to establish general relationships may be quite equal to that required for later analysis. It is so easy today to interpret the apparent rising of the sun and the difference between star and planet that we are likely to forget the care and effort, let alone the courage, that provided us with what are now commonplace explanations. Further, such commonplace is still basic and indispensable science. The men who manipulated the crude astrolabes and telescopes of the 16th century should not, in all fairness, be accused of a lower order of scientific activity than those who today command the services of electronic instruments. If we must have an order of respect, it should rank highest those who did the most with the least of facilities and accumulated knowledge.

What is true of astronomy ought likewise apply to the study of man's more immediate environment. The basic rules of experience in geology have been developed at an incalculable cost of effort. And though they can be simply stated, they are still far from being properly understood and appreciated. A recent volume by Gilbert White (1958) lists an appalling amount of evidence to show how widely the hazards of flood-plain utilization are being disregarded throughout the nation. Meanwhile secondary school pupils speak knowingly of Geiger counters and jet propulsion.

If now we come to ecology, which treats of the system of life and environment, the situation is even worse. Many leading colleges and universities do not teach it, or if they do, reserve it as a specialized course for biological majors, to be taken toward the close of an obstacle race of prerequisites. A quick examination of catalogs shows that five out of twelve leading colleges offer no ecology whatsoever, while the same thing is true of three out of eleven universities whose course listings were at hand.

It happens that for several decades it has been my task to explain the principles of this subject to many people who have had little or no previous training in biology. The fact that this can be done is no reflection on its scientific importance, or on the proper status of those who labor in this field. The fact that such knowledge is not as yet the common property of educated men and women is inexcusable. It is also costly in economic and aesthetic terms, for unless we understand the immediate system of which we are a part, we can neither manage it wisely nor enjoy it.

Let me be quite specific as to some ecological principles that should be matters of common knowledge. Life has been shaped by environment as well as its own innate properties. Man is the recent beneficiary of a highly specialized environment, on a planet some three thousand times older than he is. Plants and animals exist in living communities, whose structure and composition is an indicator of physical conditions. Recently, in demonstrating the method of pollen analysis to a group of students in Tacoma,

Washington, we were able to say that the sample of peat used must have come from a supply house in eastern United States, for it contained beech, alder, birch and linden, but no conifers.

Initially, living communities are largely under the control of raw physical environment. As they develop, they participate more and more in determining the environment, approaching a thermodynamic steady state. At this level there is an orderly recycling of materials and energy in a system that maintains itself in working condition. Human technology can either simulate or destroy such an equilibrium, depending upon the actions and values inherent in the particular culture. And again it is possible, through an understanding of the ecosystem, or more simply, the living landscape, to diagnose its condition, gauge its efficiency and tell whether it is improving or deteriorating.

Further, the study of population dynamics is an important aspect of ecology. The principle is well established that no species can possibly multiply at its theoretical rate, but must instead come to terms with the limitations of its environment (Park, 1954). A gratifying development has been the very recent lifting of powerful taboos against the discussion of this principle as it applies to man. To assume, as is common, that humanity can continue without limit to multiply in numbers and demands upon environment is counter to all ecological experience. This assumption rests upon the same fundamental fallacy that used to inspire the would-be inventors of perpetual motion machines, but until basic ecological truths become common property, the boosters of population growth and ever more lavish consumption are likely to have their way.

Simply though these principles can be stated, the intellectual and technical challenge to test them and pursue their implications will call for the same high order of ability now so manifest in more spectacular fields of science. If it be objected that the major discoveries as to community structure, composition and succession have already been made, we must reply that the task is by no means finished. There are still vast areas to be examined critically. Jack Harlan of the USDA and Oklahoma Experiment Station has this to say on the basis of extensive experience in the introduction and testing of economic grassland species:

"Plant ecology can be of great value in characterizing the types of plants we need for better grasslands. Unfortunately, the science still leaves much to be desired in the way of objective and critical interpretation of vegetation and serial succession." (Harlan, 1959.)

In more populous parts of the earth natural communities are fast vanishing, and we have no better models against which to check the efficiency of our own patterns of land use or the soundness of our attempts to classify climates and soils. Natural vegetation is still the best integrator of both that we have. Since ecology deals primarily with process, we cannot afford to break the continuity of our observations. Even in such well known communities as the grasslands, the persisting studies of Weaver, Albertson and their associates are yielding invaluable information as to the inherent resilience of this system (Weaver and Albertson, 1956).

The primary intellectual function of science is to afford us perspective and insight. But the benefits of ecology do not cease here. In a very practical way they contribute to human use and enjoyment; to use, by giving us a guide as to our inescapable part in the ecosystem and our responsibility for proper management of it; to enjoyment, by diffusing an understanding and appreciation of the world around us. Inevitably our economy must become less consumptive of material goods than it is now. When this happens we must, as both Ordway (1953) and Galbraith (1958) have pointed out, learn to derive satisfaction in new ways that do not disrupt and deplete our economic base. In the capacity to observe and appreciate our surroundings we have an almost unlimited opportunity for sound satisfaction, as any good naturalist, professional or amateur, can testify.

We cannot expect the benefits of ecology, like those of the physical and engineering sciences, to be developed through ordinary commercial channels. They must come instead by the diffusion of a better general understanding that will lead to acceptance. They should become part of the normal working equipment of those professions now operating so powerfully to change our landscape and mode of living. And equally they must become familiar to the average citizen who, under our form of society, is responsible for decisions. Whether the powerful technology now at our disposal will enrich or impoverish us depends upon the degree to which its application is governed by sound ecological principles.

In conclusion I can do no better than repeat the concluding words of an invitation paper, undelivered because of war-time conditions, but published in the AMERICAN NATURALIST (Sears, 1944):

"The ecologist, more than any other worker in biology, continues the tradition of the naturalist as exemplified by Charles Darwin. Whether he is content to accept the designation of naturalist is not important. A definition is, after all, merely an invitation to accept a term in a certain, defined sense. I should like to invite him, since the term is already in practice restricted from its classical meaning, to consider himself a naturalist. No one can compel him to do so.

"But I should further like to invite the American Society of Naturalists to extend to him, whatever he may choose to call himself, the same encouragement and active assistance which has, in the past four decades, wrought such magic within the 'grand and almost untrodden field of inquiry ... on ... variation.' "

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INTERACTIONS IN INSECT POPULATIONS*

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There is little doubt that insects as a group are the most abundant, both in numbers and in species, of the macroscopic fauna of the majority of terrestrial communities. Their small size and adaptive exoskeleton allowed them to take advantage of the many ecological opportunities presented by the great diversity of community habitats, and therefore to fill many niches at all trophic levels. The great diversity of habitats also results in a complex mosaic pattern of the physical environment which is continually altered from time to time at any given point and from point to point at any given time. Therefore, when the actions of the insects themselves, the modifications of these actions by the physical environment, and the co-actions among the various species are considered, it is apparent that the number of interactions that occur in a community is very large. And when each interaction is described in quantitative terms the number becomes almost infinite. Though each interaction is of interest in itself as a natural event, it is the types of interaction into which this great array can be classified on which attention has mainly centered because the types of interaction that occur in natural communities form the basis for a description and analysis of many of the processes that determine community structure.

When the numbers of an appropriate stage of an insect species are recorded annually it is apparent that the fluctuations in numbers are much less than the remarkable powers of increase possessed by most species would permit, and that the increases and decreases in population numbers tend to cancel each other over a period of ecological (as opposed to geological or astronomical) time without major climatic alterations. This relative stability in population density is usually taken as an indication that the abundance of each species is controlled in some manner. As deaths tend to equal births in a relatively stable population and as little relation has been found between population density and the intrinsic rate of increase of each species (Smith, 1935), the analysis of population control has centered on the many interactions that produce mortality during the life history of the insect. A very complete discussion of the natural control of insect population densities has occurred in the last decade, as indicated by, for example, the textbooks: Allee et al., 1949; Andrewartha and Birch, 1954; and Bodenheimer, 1958; two symposia: *The Numbers of Man and Animals*,

1955; and *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 1957; and the first three volumes of the *Annual Review of Entomology*: Thompson, 1956; Solomon, 1957; and Nicholson, 1958. Moreover, these verbal discussions are being supplemented, and probably will be replaced, to some extent by mathematical models, as indicated by the analysis of parasitism in a natural population (Miller, 1959) based on the model of Watt (1959).

There is a wide divergence of views among the many interpretations of the manner in which the size of populations is determined by the interactions that result in mortality. This is not surprising as there is probably more than one system of population dynamics—each resulting in different growth-forms—and the intensity of the action of the various mortality agents varies as one goes from the tropics to the poles. It is impossible, therefore, to summarize the theories of natural control without a great deal of oversimplification. The basic divergence in views appears to center around differences in the interpretation of the nature of the population itself, that is, whether or not the population is a natural entity or a statistical concept, and many other differences flow from this conflict of opinion. If the population is considered to be a natural entity it will have characteristics peculiar to itself, such as birth and death rates. Another very important property is the range of variability of each important characteristic, as this range determines what portion of the population adapts itself to increasing pressures from the environment. Some of the lethal interactions result from actions of unfavorable physical factors whereas others result from reaction of the environment induced by activities of the population itself. Thus, the population plays an active role in determining its size because the intensity of environmental reaction depends on the size of the population, that is, some lethal interactions are density-dependent or, in the newer terminology, density-governing. It is considered that only density-dependent interactions are capable of regulating density as only these, in contrast to those whose effects are independent of population density, are affected by population size. It should be noted that "regulate" means that the numbers of an appropriate stage (after, presumably, significant density-dependent interactions have occurred) of an insect are held within a greatly restricted range from generation to generation or from year to year except for modifications that may result from a changing environment.

If, on the other hand, the population is considered to be a statistical concept then it is merely a collection of individuals, each of which is subjected to all the interactions of a physical nature which change from time to time and from place to place. These interactions not only produce catastrophic effects but they control the quantity and quality of necessities such as the food supply. Thus the increase and decrease in population size can result from the favorability or unfavorability of the environment. The properties of the environment are affected both by aperiodic or random variations and by long-term trends in weather cycles, or possibly by extra-terrestrial influences. Thus the population plays a passive role in the determination of its own size and the control of its size can, therefore, be the result of

density-independent interactions alone. It should be noted that "control" in this context often refers to the determination of a seasonal peak of abundance and that emphasis is placed on the pattern of mortality within generations or seasons.

It is obvious that the degree and speed with which the various mortality agents respond to variation in population density have a considerable range. But in general most of the biotic agents are usually considered to be density-dependent in action whereas the climatic factors act independently of population size. Of course the two groups of factors act concurrently and in sequence so that the net effects of a factor of one type are often masked by the magnitude of one of the other.

The ability of the biotic agents to influence population density can be modified in several ways. First, the biotic agents interact with each other. Park (1948) showed that the results of competition between *Tribolium confusum* Duval and *Tribolium castaneum* Herbst depend on the presence or absence of the protozoan parasite, *Adelina tribolii* Bhatia. Second, the mortality caused by the biotic factors of the environment may follow a stochastic rather than deterministic course. Skellam (1955), for example, predicted that all density-dependent processes will usually lead to extinction of the population if they are carried on for a sufficiently long period. Third, as insects are poikilotherms the effects of the physical environment not only affect their toleration physiology and food supply but also the intensity of the density-dependent interactions. This last aspect could be of great significance, quantitatively, because either short aperiodic or long-term trends in weather would greatly modify the influence of the biotic agents and presumably impress their cycles on any that might be inherent in the interaction. To amplify this under-emphasized aspect of population dynamics it is proposed to indicate how one biotic interaction—that between host and parasite—is modified by one physical factor—temperature. Before the influence of a physical factor on the interaction can be discussed it is necessary to describe the interaction of host and parasite.

HOST-PARASITE INTERACTION

One useful method of analyzing the exceptionally complex and intricate processes that occur in communities is to remove species from their natural habitats and propagate them under controlled conditions. Experimental populations are not, of course, counterparts of natural populations but they permit an examination of how certain processes occur and the populations can be made more complex by the introduction of additional variables, one at a time. As Insecta contains species which have only one generation each year and other species which have two or more generations, often overlapping, each season, experimental populations have been developed for the study of host-parasite interaction in which the generations of host and parasite are discrete while in others they overlap.

Host-parasite populations with discrete generations. The growth-forms of host and parasite populations in which each generation is distinct can be

simulated by arbitrarily restricting the powers of increase of both species. The parasite is allowed to search for sedentary hosts for a limited period only. Each parasitized host is considered to produce one thelyotokous female parasite whereas each unparasitized host produces a small number of hosts in the next generation. This technique, developed by DeBach and Smith (1941), was used to establish the growth-forms of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.), and its chalcid parasite *Encarsia formosa* Gahan (Burnett, 1956). Parasite females searched for hosts, distributed over a flat surface slightly more than 400 square inches in area, for 18 hours at 24°C. The rate of increase of the host was two. The experiment was begun by allowing 11 parasites to search for 22 hosts and continued for 21 "generations." The results of each generation were obtained from the average of ten replicates. During the 21 generations the numbers of both hosts and parasites passed through two oscillations of increasing amplitude before the average of the parasites was reduced below one individual. As Nicholson and Bailey (1935) predicted oscillations of increasing magnitude as a result of host-parasite interaction, the empirical results were tested against their theoretical equations. Although there were obvious differences between observed and theoretical results the general trend was reasonably (but probably not statistically) close to expectation. The differences arose from a number of causes: the "area of discovery" was not a constant, as required (see below); the properties of the animals no doubt changed slightly during the three-month duration of the experiment (see below); although each generation was replicated ten times, small chance variations probably were magnified in later generations; and the value of the statistic, the "area of discovery," is very sensitive so that slight differences in computation may have strong effect on the calculated curves.

Host-parasite populations with overlapping generations. The growth-forms of freely-interacting populations with overlapping generations were recorded when *T. vaporariorum* and *E. formosa* were propagated on 96 tomato plants for eight months (Burnett, 1960). Although there were some differences in the growth-forms among eight experiments, in all cases the numbers of adult hosts and parasites showed fluctuations of increasing magnitude. The differences in growth-forms consisted principally of variation in the magnitude of some peaks of host numbers (ranging from absence to approximately 45,000 (unpublished data)) and in the average densities of the populations. These differences appear to result from variation in the densities and age structures of the populations at the beginning of the experiments and warrant further investigation.

A comparison of the growth-forms of populations with overlapping generations and those with discrete generations shows that the former differed from the latter in at least two respects. First, with discrete generations the minimal values of the fluctuations were successively lower whereas with overlapping generations they were either sub-equal or successively higher. Second, the growth-forms of populations with overlapping generations were more complex than those of populations with discrete genera-

tions. As the results obtained by using populations with discrete genera-
tions were, by the design of the experiment, determined only by the effects
of host and parasite densities on the growth rates of their populations, addi-
tional variables must have been operating in the populations with overlap-
ping generations. One such variable was the mortality of host larvae that
occurs at high parasite densities. As dead larvae produce neither hosts nor
parasites the parasite population decreases much more rapidly than if all
parasitized hosts produced parasites; and thus a higher proportion of the
host population in the next generation escapes attack. This type of modifi-
cation tends to dampen the fluctuations which arise primarily from the ef-
fect of variations in host and parasite densities on the rate of growth of
host and parasite populations.

EFFECTS OF TEMPERATURE ON HOST-PARASITE INTERACTION

It is necessary to evaluate the effect of a physical factor such as temper-
ature on discrete phases of the host-parasite interaction if an indication of
the differential response of a host and parasite species to a variable en-
vironment is to be obtained in quantitative terms.

Toleration. The influence of climatic extremes on populations of the
oyster-shell scale, *Lepidosaphes ulmi* (L.), its parasite *Aphytis mytilas-
pidis* (LeB.), and its acarine predator *Hemisarcoptes malus* (Shimer) was
determined in Nova Scotia and New Brunswick by Lord and MacPhee (1953).
In Nova Scotia the winters are mild and both parasite and predator survived
to control the host. In the coastal areas of New Brunswick winter tempera-
tures range as low as $-27°C.$ to $-29°C.$ every year or so, and under these
conditions mortality of the parasite was higher than that of the mite but be-
cause the parasite had three generations per year it soon recovered suffi-
ciently to be an important factor in the control of the host. In Central New
Brunswick, however, winter temperatures are $-29°C.$ or lower and, as the
parasite could not survive these conditions, the main agent of control was
the predacious mite. The differential survival of the three species was ex-
amined in the laboratory and the resistance of the overwintering forms of
the host and parasite—the eggs of *L. ulmi* and larvae of *A. mytilaspidis*
—was summarized by Lord and MacPhee in figure 3 C of their paper. From
this figure it is clear that at all temperatures much longer exposures were
necessary to produce 90 per cent mortality of the sample populations of the
host than of the parasite—even temperatures as low as $-32°C.$ The mite
appeared to be cold resistant. In this example a catastrophic mortality fac-
tor, instead of contributing to host-parasite fluctuation, determined, accord-
ing to Lord and MacPhee, which biotic agent controlled the insect pest.

Development. The differential effects of temperature on the autecology
of the greenhouse whitefly, *T. vaporariorum*, and its parasite *E. formosa*
(Burnett, 1949, table 7) leads one to expect that the rate of increase of the
parasite population in relation to that of the host population would become
progressively greater with increase in temperature. The validity of this was
examined when populations of *T. vaporariorum* and *E. formosa* were propa-

gated on tomato plants (four host plants for each population) at 18, 24, and 27°C. At 18°C. the host population increased at a much faster rate than did that of the parasite, and it was obvious that the number of hosts that the host plants could support was the factor limiting the density of *T. vaporariorum*. At 24°C. the parasite was able to reduce the density of the host to a low level by the 120th day of the experiment, but before this there were fluctuations in the numbers of host and parasite. These fluctuations were determined in part by the single introduction, followed by rapid death, of the parasite populations (causing some discreteness of generations), but fluctuations inherent in the host-parasite relation no doubt played their part toward the end of the experiments. At 27°C. the parasite quickly reduced the host density and though there were fluctuations in the numbers of host and parasite these occurred at much lower levels than in the experiment at 24°C.

These results indicate that the physical environment modifies the properties of both host and parasite species so that there is a limited range of conditions within which the parasite, by itself, is able to prevent the uninterrupted increase in the numbers of the host species. In addition, it seems likely that within this range the densities of host and parasite vary with variation in temperature.

Response. The distribution of host and parasite populations results, no doubt, from a complex of factors of both the physical and biotic environments. That the populations of *T. vaporariorum* and *E. formosa* do not completely coincide, even in the relatively uniform environment of a greenhouse, became evident in a study on the dispersion of these two insects (Burnett, 1948). One factor that could result in a differential distribution of host and parasite was the differential response of the two species to a range of temperatures in the area in which they were breeding. To examine this possibility, sample populations of host and parasite were introduced, separately, into a temperature gradient. The modal temperatures recorded for each species are of no importance when considered separately but a comparison of the two sets of readings indicates significant differences in behavior. Although both sample populations moved from the warm to the cold portion of the temperature gradient during a period of 72 hours, there were two aspects in which the movement of host and parasite differed: (a) the parasite population gradually moved down the gradient over the 72-hour period whereas the host population moved from the warm to cold end of the gradient during the first 24 hours; and (b) the modal temperature of the parasite females at any given time of the experiment varied with the temperature at which the parasite population was reared in the greenhouse, whereas that of the host was independent of rearing temperature. These differences in behavior were not determined either by a differential response to the humidity gradient associated with the temperature gradient or by a combination of random movement and a trapping effect of the cold end of the gradient. The results suggest that in nature temperature is one of the environmental factors that tend to separate partially host and parasite populations.

Searching. The differential survival, development and dispersion of host and parasite populations are phases of population ecology that deal primarily with the direct effects of the physical environment on the separate populations. It is the co-actions of host and parasite populations, however, that need to be determined if the role of parasites in the regulation of host density is to be established. A co-action of primary importance is the ability of the parasite population to find and to parasitize hosts, and it is therefore necessary to examine how this faculty is modified by variation in the physical environment.

The direct effect of temperature on the ability of an insect parasite to find and parasitize its hosts was determined when the chalcid parasite *Dahlbominus fuscipennis* (Zett.) searched for cocoons of conifer-infesting sawflies, *Neodiprion* spp., distributed over flat surfaces in laboratory, seminatural, and natural environments. In laboratory experiments a constant number of *D. fuscipennis* searched, at 16, 20, and 24°C., for a constant number of hosts distributed over different areas (Burnett, 1951). As the individual female does not attack more than two cocoons in its lifetime (Ullyett, 1936), it is not surprising that the increase in parasitism became progressively much less with increase in host density. Variation in density, however, was not the only factor that determined the number of hosts attacked because at each density parasitism varied with temperature; for example, at the highest density the parasite population found over twice as many hosts at 24°C. as it did at 16°C. The validity of the laboratory results was confirmed when the parasites searched for hosts distributed over 25-square-foot plots of grass lawn under naturally varying temperatures (Burnett, 1954) and also when they searched for cocoons distributed over 24-foot square field plots (Burnett, 1958c). The three groups of curves have been described by equations—more complex than those used hitherto—developed by Watt (1959) and by Holling (1959).

An indirect effect of temperature on the ability of an insect parasite to find and parasitize hosts was revealed in a number of laboratory experiments in which a constant number of *E. formosa* adults searched for various numbers of *T. vaporariorum* distributed uniformly over 25-square-inch flat surfaces. The insects used in the first set of experiments were propagated in temperatures that were low and variable. Although the parasites tended to find hosts in proportion to the number present (the relation was not strictly linear) they attacked only about 50 per cent of those exposed, and the females laid about four eggs at the highest host density (Burnett, 1958a). The insects used in the second set of experiments searched for hosts under the same conditions as those used in the first, but they were reared at temperatures which were high and relatively stable. Again the parasite tended to find hosts in proportion to the number exposed (the relation was not strictly linear) but in this instance over 80 per cent of the hosts exposed were attacked and each female laid about eight eggs at the highest host density (Burnett, 1958b). These experiments indicate that the rearing temperature of a host and parasite population can influence the searching ability of the

parasites.   Whether the effect is produced through modification of either
host or parasite or of both species is not known.

The searching experiments with *E. formosa* and *D. fuscipennis* illustrate
another important aspect of parasitism. In both the populations with dis-
crete generations and in the freely-interacting populations with overlapping
generations a greater number of hosts were parasitized as more hosts were
exposed to the parasites. In the following generation more parasites were,
therefore, searching for hosts, so that the percentage of hosts parasitized
increased. In this case, the proportion of hosts parasitized gradually in-
creased or decreased over a number of generations and there was a lag in
the response of the parasite population to change in host density. However,
when 20 females of *E. formosa* searched for various numbers of *T. vaporari-
orum* distributed over a 200-square-inch area the percentage of hosts para-
sitized increased from 40 to 68 as the number of hosts exposed was in-
creased from four to 36 (Burnett, 1958b, table 1). And a comparison of the
parasitism among constant numbers of cocoons of *Neodiprion* sp. placed ad-
jacent to four different densities of the same host suggests that *D. fusci-
pennis* females are attracted to the higher densities of its host (Burnett,
1958c, table 2). In both these latter cases the parasite population was able
to respond to increased host density within a generation. However, these
mechanisms appear to operate over a narrow range of host density and they
may not be sufficiently effective, without an increase in the total number of
parasites, to prevent growth of the host population.

Insectary population. It is apparent that variations in temperature modify
many discrete aspects of host-parasite interaction. The question naturally
arises as to whether or not the growth of host and parasite populations are
significantly influenced by the seasonal temperature cycle. To examine this
question *T. vaporariorum* and *E. formosa* were propagated in an insectary
under naturally varying temperatures. The host-parasite population was
reared on 56 tomato plants with aid of supplementary fluorescent lighting.
One-quarter of the host plants were changed every two weeks so that a
supply of fresh foliage was always available to the host insect. Thirty-
three hundred adults of *T. vaporariorum* were released among the plants over
a one-month period and 2200 adult parasites were added when susceptible
hosts were present over a two-week period. All the adults of both species
were counted twice a week from May 14th to the end of September. A record
of the temperature inside the insectary was kept during the experiment.

The total numbers of adult hosts and parasites counted twice a week and
the average daily temperatures are shown in figure 1. The average tempera-
tures were 18°C. or lower until Day 42. During this period many of the orig-
inal adult hosts and parasites must have dispersed from the host plants, be-
cause the numbers counted were less than one-half of those introduced. The
host population developed very slowly at the low temperatures; the first in-
crease shown in figure 1 resulted from the introduction of 2,000 individuals.
The parasite did not limit the increase of the host until about Day 50 when
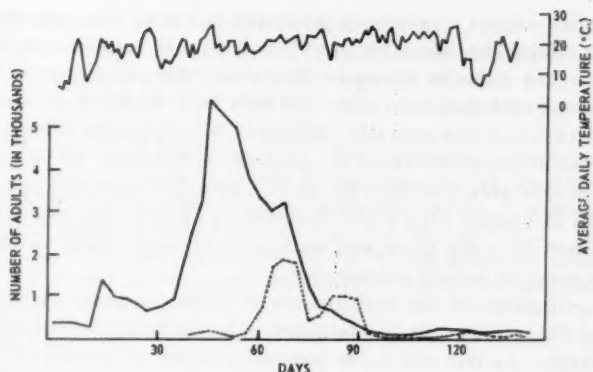the average (but not constant) temperatures were approximately 18°C. Sub-

FIGURE 1. Numbers of adult *T. vaporariorum* and adult *E. formosa* counted twice a week when this host and parasite were propagated on 56 tomato plants under naturally varying temperatures. Upper solid line: average daily temperature. Lower solid line: numbers of adult *T. vaporariorum*. Broken line: numbers of adult *E. formosa*.

sequently, with temperatures of 21°C. or higher, the parasite reduced the host density and the numbers of both species fluctuated at very low levels for the rest of the experiment.

Figure 1 shows the numbers of adult hosts and parasites present—not those that emerged (because the adult host lives much longer than the adult parasite). The high percentage of host larvae observed to be parasitized, from Days 40–50 until the end of the experiment, indicates that the parasite population controlled the growth of the host population. The effect of variation in temperature was not to determine the numbers of the host species directly but to modify the interaction of host and parasite populations. It is interesting to note that when the parasite controlled the host population the numbers of both host and parasite were relatively stable for an appreciable period of time.

CONCLUSIONS

Fluctuations in the numbers of hosts and parasites seem to be inherent in the interaction of host and parasite populations, with the nature of the fluctuations determined by several biotic factors. The relation between host and parasite is modified, however, by variation in a physical factor of the environment, such as temperature. Low lethal temperatures often determine which species of parasite exist in a given area. The dispersion of host and parasite populations may not completely overlap in the presence of temperature gradients. Temperature controls the rate of increase of host and parasite populations and modifies the ability of insect parasites to find and parasitize their hosts. As indicated to some extent in figure 1, seasonal temperature cycles vary the emphasis of discrete aspects of host-parasite interaction and thus modify the fluctuations in numbers and average densities of host and parasite populations.

The limited amount of evidence presented indicates that temperature differentially affects the toleration, developmental, and response physiology of insect host and parasite species. Therefore, the co-actions of host and parasite, measured quantitatively, will vary with variation in temperature. The modification of host-parasite interaction by temperature change is merely one example of the influence of the physical environment on biotic interactions but it indicates that both the short, aperiodic variations and the long-term trends in weather affect each herbivorous species not only directly but also by controlling the types and intensities of many of the biotic interactions that occur in natural communities.

The significance of the modification of biotic interactions depends, of course, on the role that these interactions play in the determination of population density. As this role is, at present, a matter of controversy, a definitive judgment cannot be made. But in view of the sensitivity of biotic interaction to environmental change the obviously close relationship between population density and weather may be indirect.

SUMMARY

Temperature differentially affects the toleration, developmental, and response physiology of host and parasite species and therefore modifies the co-actions of host-parasite populations. This example of the influence of a physical agent on host-parasite interaction indicates that the changing physical environment can control the types and intensities of many of the biotic interactions that occur in natural communities.

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ECOLOGICAL ENERGY RELATIONSHIPS AT THE
POPULATION LEVEL*

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I will be concerned with the ecologically significant energy relationships of single species populations. The theoretical analysis and data deal primarily with laboratory populations of *Daphnia pulex*, but I believe that the conclusions have significance for nature as will be indicated in the discussion.

The number and kind of organisms found in nature is variable from year to year and even from day to day. Despite this variability, it can be said that a sufficiently detailed and temporally extensive examination of any one species, or even of an isolated population of a species, will show that the number of organisms and volume of protoplasm represented by that species or population remain approximately constant. Some populations may vary in size in a cyclic way, either annually or possibly with some other period; others may vary in a random way, but in any case there is some definite mean population size, if data over a period of the order of ten times the mean generation time is considered.

Mean population size does not represent an equilibrium value in the sense that the position of a pendulum bob at rest represents an equilibrium, but rather represents a steady state. The steady state can be characterized by the fact that it requires energy for its maintenance. Just as the steady state temperature gradients in a metal bar heated at one end would disappear in the absence of an energy source, so the steady state properties of the ecological world would vanish in the absence of the radiant energy of sunlight.

It is possible to conceive of a series of metal bars in contact at their ends, with the terminal bar converting radiant energy into heat and this heat then being transmitted by conduction through the whole series of bars. Again a steady state temperature gradient would characterize each bar. Similarly in nature radiant energy is converted into potential energy by the green plants and this potential energy is transmitted through a chain of organisms. There will be various steady state values characterizing this chain of organisms. We will be concerned with some of the values that are more or less immediately recognizable as functions of energy, in particular the potential energy, contained in the various single species populations, that is, the standing crops, and with the ratios between the various steady state rates of energy transfer in the system, that is, the efficiencies (Lindeman, 1942).

I have confined myself to steady state values since a short period of very high ecological efficiency or standing crop maintenance has very little applicability to long term values that are likely to occur in nature. Non-steady state efficiencies or standing crops must eventually receive intensive study, but I feel that more immediate progress will be made by considering them as minor perturbations of the steady state values for the moment.

Examining the analogy between metal bars, electric wires, flowing water and other inanimate models on one hand and an ecological community on the other, it is seen that the analogy breaks down almost immediately. In a heat transmission system or in an electric wiring diagram the continued physical existence of the energy transmitting elements is not contingent on the maintenance of energy flow. In a biological system, if energy flow ceases there is almost immediate dissolution of the system's components.

The process of energy flow in ecological systems does not lend itself to discussion in terms of gradients or flow diagrams, except on the most rudimentary level. Flow diagrams are primarily suitable to discussion of heat or radiant energy transport in which physical contact or simply suitable geometric distribution of the physical elements will permit energy flow to occur. In ecological interactions the energy involved is in the form of potential energy, which in general can not be transmitted between parts of a system without displacement or distortion of the physical elements. That is, energy flows from a plant population to an animal population only when a concrete plant or piece of plant is physically removed into the body of some particular animal. It only remains for the ecologist, if he is to concern himself with energy at all, to develop his theories and concepts on a biological basis rather than by assuming the direct applicability of the laws developed for the simple systems of physics and electronics.

Even such elementary concepts as efficiency and energy, and such universal generalizations as the second law of thermodynamics have very peculiar properties on the level of the ecological community.

I will therefore discuss the concepts of efficiency, energy and entropy as they apply to ecology. Ecological efficiency will then be shown to have at least three distinct, operationally defined meanings. These three different concepts of efficiency will be evaluated from the data on *Daphnia pulex*. I will then suggest that certain kinds of efficiency are actually constant for most populations in nature. I will finish with some speculations on the relation between energetics and the future development of a complete theory of community ecology.

AN ELEMENTARY CLARIFICATION OF EFFICIENCY, ENTROPY AND ENERGY IN ECOLOGICAL SYSTEMS

The superficial simplicity of the concept of ecological efficiency requires careful analysis.

The efficiency of an energy machine is easy to define. A machine, in general, is designed and constructed to do a particular kind of work or to produce a particular form of energy. The ratio of the output to the input (both in energy units) is the efficiency of the machine. The output of a mov-

ing locomotive is in energy used to overcome the forces that tend to stop the train; the input is in the potential energy of coal or oil burned in the process. The output of a light bulb is in visible radiation; the input in electrical energy and the ratio of the two is the efficiency. But notice that it is possible to read by the light of a coal locomotive's fire box or to warm oneself at a cloth-draped light bulb. These do not seem particularly clever ways to read or to keep warm, but they are conceivable. From the standpoint of a moronic bookworm the efficiency of a locomotive might be measured as the ratio of visible radiant energy from the fire box to potential energy consumption. For most locomotives this efficiency is lower than our initial calculations of the efficiency of the locomotive. Our chilled illiterate in front of the draped light bulb might measure efficiency as total radiant energy output over total electrical energy input and this ratio would be higher than our original estimate of the efficiency of the bulb. I conclude from this that the magnitude of an efficiency need have nothing to do with the importance of the process to which the efficiency ratio refers, even in the case of a machine.

An organism must do many things that require energy. Movement of its internal parts, movement of itself in its environment, producing new protoplasm to compensate for attrition of its own body, adding new protoplasm to its own body and producing offspring are all energy utilizing processes involving single organisms. On the level of the individual we will be concerned with the efficiency of the last two of these only.

This limitation of our concern is due to a peculiar property of ecological interactions. In order to maintain an ecological community of several kinds of animals and plants at a steady state, the new protoplasm made by any population of organisms of any one species, above and beyond replacement requirements, must be consumed during the process of maintaining the steady state of one or more of the other species present. The new protoplasm produced by any population is in one sense a sum of the new growth occurring in all the individuals of that population. I will therefore consider only new protoplasm to be an ecologically useful kind of potential energy and will largely ignore other possible uses of energy on the individual level.

It is impossible to refer to *the efficiency* of a population. The term must, at all times, be qualified. We can speak only of the efficiency of producing energy in some form which we arbitrarily consider useful (the output) from some other form which we arbitrarily define as useless (the input).

The concept of energy is used rather loosely in ecological literature, and recently the concepts of entropy, negative entropy and information have been used equally loosely. We have statements in print that organisms live on order or that communities consume negative entropy, eat information, etc. It therefore seems appropriate to present a statement of the role of energy in ecology.

Radiant energy is absorbed by green plants and part of this is converted to potential energy by the process of photosynthesis. The slow conversion of this potential energy to kinetic energy permits ecological communities to survive.

Particular compounds in the plant will be converted into other compounds in the herbivore. To the extent that individual reversible chemical reactions are being considered the various terms in the equation

(1) $$\Delta H = \Delta F + T \Delta S$$

may be evaluated and the change in entropy per mole computed. An appropriate summation of the entropy contributions of all the reactions that occur in the process of incorporating plant material into the herbivore might be considered the entropy production of the herbivore, were it not that:

1. All of the reactions tend to interact with each other.
2. Phase differences and structural restrictions of complicated kinds occur in both plants and animals and the reactions producing these phase differences are, in general, not reversible in any practical sense, at least in the aggregate.

In other words, it is very difficult by simply supplying energy to get an organism to undigest a meal and thereby measure the ΔF associated with the digestion process. The entropy associated with the process of food assimilation is therefore not conveniently measurable.

It is possible to consider the state of all materials entering an organism and the state of the material leaving the organism, duplicate the degradation process in a reversible way and make the appropriate entropy calculation. To my knowledge this has never been explicitly done for all of the ingested and waste products of any particular organism. It is clear, in principle, that it could be done and if it were done we would find an increase in entropy associated with this passage through the organism as illustrated:

$$\Delta H \rightarrow \boxed{\text{organism}} \rightarrow \Delta F + T \Delta S + Q'$$

(2) $$\Delta H = \Delta F + Q' + T \Delta S$$

This requires explication. ΔH can be defined as calories ingested per unit time and ΔF in this context is the calories egested which are still of use to organisms as a supply of energy. $T \Delta S + Q'$ are the caloric equivalent of the heat produced in the utilization of the energy ΔH.

$T \Delta S$ is the heat that would be produced in the various transformations occurring in the organism on the assumption that all reactions were reversible, independent, and of infinitely slow occurrence. None of these conditions is met.

Q' is the heat produced from friction within the organism and from work done by the organism on its environment. In principle, Q' can be evaluated experimentally, but the problem is technically difficult; and except for very simple systems is not likely to be done. It is possible, in an ecological steady state, to write the equation:

Caloric equivalent of the potential energy ingested = caloric equivalent of the potential energy removed from the population by egestion, predation, mortality, etc., plus the heat produced by the population.

It may be legitimate to equate this heat to entropy, but it is not clear what proportion of the potential energy ingested actually shows up as entropy. Estimates of anywhere from two to 50 per cent might be offered.

The notion of entropy content of a living organism is extremely complex. Normal thermodynamic theories apply to an equilibrium state, which is equivalent in one sense to death. The theory of thermodynamics of steady states (Denbigh, 1951) is not yet capable of handling elaborate multiphasic systems. The Onsager equations which permit some development of steady state thermodynamics depend on the rigorous definition of fluxes and on their associated forces.

Any energy gradient of an appropriate sort can be considered a generalized force. This is particularly evident in the relation between a temperature gradient and heat flow. The interesting ecological energy flow is in the form of potential energy. Potential energy can have a gradient, as in the glucose gradient in a single cell. Ecologically, however, the gradient is a rather coarse histogram, of standing crop vs. trophic level. The precise procedure for the interpretation of this histogram as a generalized force seems unclear.

The fluxes can, therefore, be stated but the forces can only be dealt with on an almost metaphorical level in ecology. While metaphor leads to certain sorts of insight it does not have predictive power.

A further complication in the application of thermodynamics to steady state systems has been considered by Foster, Rappoport and Trucco (1957) who find that Prigogine's theorem, which states that steady state systems tend to a condition of minimum entropy production, is not applicable to certain types of feedback systems. It is now generally conceded that individual organisms, populations of organisms, and natural communities must be treated as complex feedback systems and it is quite likely that Prigogine's theorem does not apply to ecological systems, or at least its validity can not simply be assumed.

Potential energy (ΔH) can be approximately measured by direct combustion of dried tissue. A certain amount of entropy ought to be subtracted from the combustion calories but this is not practical for reasons indicated above. Some free energy is lost prior to combustion in the drying process but this has not yet been evaluated.

When I speak of the energy content of an organism I will be referring to the calories released by burning that organism under normal atmospheric conditions and measured as heat. This is equal to the difference in potential energy per gram between dried protoplasm and the various oxidation products of that protoplasm and includes both the free energy and the entropy.

When I refer to a flow of energy through a population I will be considering only the steady state in which the rate of energy accumulation is zero.

THEORY OF ECOLOGICAL EFFICIENCIES AND THEIR INTER. IONS

A population of organisms is characterized by new animals being born, by animals dying or being consumed (by other animals or by man). I will be

concerned with the potential energy content of the animals removed from the population by predators or man as a useful energy output and will consider the food consumed by the population as the energy input. That is, when I speak of ecological efficiency, I am assuming the viewpoint of a predator.

In one sense, the removal of an animal by a predator can be considered a divergence of energy from the other possible roles it might play in the population. In particular, the greater the rate at which yield is removed from the population the smaller the standing crop that the population is capable of maintaining. The yield to the predator divided by the difference between the energy used in maintaining a population in the absence of predation and that used in maintaining the same population under predation will be called the population efficiency.

The ratio of the potential energy in an individual organism to the potential energy utilized in its birth and growth will be called growth efficiency, or individual growth efficiency.

The interrelation between these three concepts of efficiency is discussed below.

The gross inflow will be in units of calories per time per volume and will be designated I_F. This will be the amount of food made available to the population from some outside source. In nature food is available to an animal population as a result of the activities of some other population or populations of plants, animals or both. In the laboratory I_F is the potential energy in the food made available to the population by the experimenter. The population does not necessarily consume all of this food. In nature part of it may pass through the ecological space of a particular population without being altered at all. In the laboratory the experimenter may periodically remove excess food.

We must therefore distinguish between I_F, the food available, and I, the energy input or ingested food. $I_F \geq I$ is always trivially valid.

I is the potential energy ingested per day per population and therefore is slightly different in concept from I_F, unless the volume considered only contains one population. In experimental situations discussed here this difference is not significant.

Population size is effectively constant at a steady state in the absence of cropping, fishing and predation. In a typical experimental study of efficiency the population is cropped and censused at regular intervals so that a plot of population size as a function of time would be saw-toothed. For our present discussion we will consider the population size as the size at the base of the saw teeth. This is equivalent to assuming that no energy must be expended in maintaining those animals which are destined to be cropped at the next census. This assumption is not dangerous so long as the ratio $\left(\dfrac{\text{yield/census interval}}{\text{population size}} \right)$ is small. (See Armstrong, 1960.)

Let P′ be the caloric content of the standing crop of a population subjected to some arbitrary predation process and let P be the caloric content of the appropriate control population in the absence of predation. P and P′
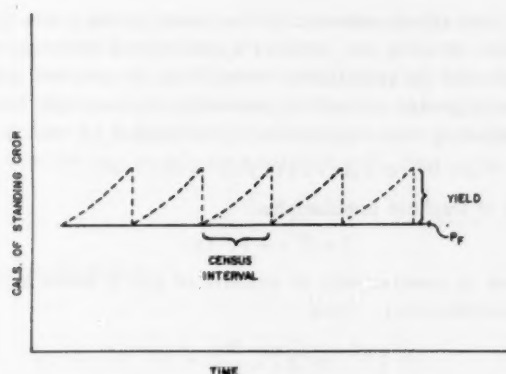
FIGURE 1. The term standing crop (P_F) is used as indicated in this diagram, ignoring the maintenance cost of the animals destined to constitute yield. A more precise but less convenient measure of standing crop would be the dotted line.

have the dimensions of calories and represent the potential energy maintained in the living protoplasm of the population. Occasionally we will use the letters P and P′ as names for populations.

In order to maintain living protoplasm, energy must be expended. The greater this energy expenditure per calorie of standing crop per time the smaller will be the value of P that can be maintained by a given energy income per day (I).

In general, increase of I will imply increase of P. The precise relation between P and I is not obvious *a priori* since the maintenance cost per calorie of standing crop may be a complicated function of the interactions between individual organisms in the population.

In the most general case, since there is a unique age distribution and total number of organisms corresponding to any steady state caloric content we can write

(3) $I = Pc + P^2 c' + P^3 c'' \ldots$

where c is the proportion of the total cost in (calories/calorie day) of maintaining one calorie of standing crop which is assignable to first order interactions in the population, c′ the proportion assignable to second order interactions, etc.

It has been experimentally demonstrated in Daphnia that only first order interactions are significant over a wide range of population densities (Slobodkin, 1954) so that for the present discussion (3) reduces to

(3′) $I = Pc$.

When a population is subjected to predation it either becomes extinct or it comes to a new steady state caloric content P′. If the population can survive steady predation potential energy now leaves the population at some steady state rate as yield to the predator. The ratio of yield (Y) in calories per day to I is the ecological efficiency.

The age and size of the individuals that make up the yield is determined by the interaction between the predator's method and intensity of capturing the yield animals and the population dynamics of the prey and predator.

Assuming that I is not altered by predation, we can take account of the change in maintenance cost associated with predation by writing

$$(4) \qquad I = P'(c + \Delta c) + (P')^2 (c' + \Delta c') + \dots .$$

and in the case of Daphnia populations

$$(4') \qquad I = P'c + P'\Delta c .$$

Assume the prey to consist only of animals of age i, taken by the predator at the rate Y_i calories/day. Then

$$(5) \qquad P'\Delta c = \frac{Y_i}{E_{pi}}$$

where E_{pi} is the efficiency, in one sense, of this predation process. An efficiency of this type will be referred to as a population efficiency. Since

$$(5') \qquad E_{pi} = \frac{Y_i}{P'\Delta c}$$

population efficiency can be interpreted as the ratio of yield of a particular kind to the increase of maintenance cost associated with the production of that yield. It will vary with the kind of organism taken as yield. It is independent of the intensity of predation so long as the linearity implicit in equation (4') holds.

The precise value of E_{pi} depends on growth and survival and their interaction with age in an intimate way which will be indicated below.

In order to clarify the meaning of E_{pi} we must examine an individual organism more closely. At the time an individual organism begins to take nourishment, say age j, it already represents the end product of a series of metabolic processes, all of which have involved the degradation of potential energy. As it grows to some arbitrary age, say i, it will consume more potential energy and may have increased its caloric content. In any case the total potential energy that must be used to replace an animal of age $i > j$ will be greater than that required to replace an animal of age j.

If we designate the total energetic cost of replacing an animal age i as $\frac{S_i}{E_i}$, in which S_i is the caloric content of the animal age i, then E_i is the growth efficiency of this animal. The caloric content (S_i) is usually proportional to the size of the animal. E_i can be evaluated as the inverse of the total calories consumed in the production of one calorie of protoplasm at age i and is the "individual growth efficiency" of an animal aged i. It varies with the age and feeding rate of the animal concerned and with the energy expended by the parents of that individual in producing it.

The concept of growth efficiency has suffered in the past from failure to specify precisely the time interval over which the growth of the animal is to be considered. Here we have taken this as the entire life span over which

an energetic cost can be meaningfully associated with the individual, following the suggestion of Armstrong (1960).

The relation between E_i and E_{pi} can be clarified as follows.

Let N_0 and N'_0 be the number of newborn animals produced per day in populations P and P' respectively, and let l_x and l'_x be the per cent survival to age x in the two populations respectively. Define q_x as

$$q_x = \frac{l_x - l_x + 1}{l_x}$$

and correspondingly define q'_x.

Also let

(6) $\qquad\qquad d_x = q_x l_x$ and similarly for d'_x

and

(7) $\qquad\qquad D_x = d_x N_0$ and similarly for D'_x.

The deaths per day in population P is $\sum_0^\infty D_x$ and in population P', $\sum_0^\infty D'_x$. The primary characteristic of a steady state population is that births and deaths are equal and there is no change in mean total biomass with time.

The caloric cost per day of replacing the dying individuals and maintaining biomass constancy is $\sum \frac{D_x S_x}{E_x}$ in population P and assuming that caloric content as a function of age and growth efficiency are both dependent on predation $\sum \frac{D'_x S'_x}{E'_x}$ in population P'.

In other words

(8) $\qquad\qquad I = \sum_0^\infty \frac{D_x S_x}{E_x} = Pc$

$$= \sum_0^\infty \frac{D'_x S'_x}{E'_x} = P'(c + \Delta c)$$

whence

(9) $\qquad\qquad c = \frac{1}{P} \sum_0^\infty \frac{D_x S_x}{E_x}$

and

(10) $\qquad\qquad \Delta c = \frac{1}{P'}\left(\sum_0^\infty \frac{D'_x S'_x}{E'_x}\right) - \frac{1}{P}\left(\sum_0^\infty \frac{D_x S_x}{E_x}\right)$

and substituting (10) in (5') we define the population efficiency of animals age i as

(11)
$$E_{pi} = \cfrac{Y_i}{\left(\displaystyle\sum_0^\infty \frac{D'_x S'_x}{E'_x}\right) - \frac{P'}{P}\left(\displaystyle\sum_0^\infty \frac{D_x S_x}{E_x}\right)}$$

or if food ingestion is constant under predation simply:

(11')
$$E_{pi} = \cfrac{Y_i}{I\left(1 - \frac{P'}{P}\right)}$$

From equation (11) it can be seen that population efficiency varies inversely with the depletion of standing crop population size associated with the removal of the yield. Decrease in life expectancy with predation also lowers population efficiency. A predator would be acting with maximum prudence if he removed yield from his prey in such a way as to maximize population efficiency.

We will return to this concept after we have considered ecological efficiency. The commonest usage of the term efficiency in ecological literature is the ratio of the energy per unit time taken from some population (the prey) as yield by some other population (the predator) to the energy per unit time ingested by the prey population. I am deliberately ignoring the often made distinction between ingestion and assimilation, since the meaning of ingestion seems fairly clear while it is an almost arbitrary matter to decide when, or what portion of, a particular mouthful of food is assimilated.

Food chain efficiency (a term borrowed from LaMont Cole) is similar to ecological efficiency except that the denominator is the food available (I_F) rather than the food ingested (I).

Ecological efficiency (E) is therefore defined by $\frac{Y}{I}$. Since population efficiency is defined for any constant predation method, if I is not changed by predation

(12)
$$E = E_p \left(1 - \frac{P'}{P}\right),$$

from which it is clear that for any predation method

(13)
$$E \leq E_p \ .$$

The relation $E = E_p$ will hold only for a scavenger or for a predator which replaces some other source of mortality. If there is any selective advantage in maintaining a large standing crop, a predator population will tend to maximize yield from its prey. This is equivalent to maximizing food chain efficiency $\left(\frac{Y}{I_F}\right)$. As predation becomes more intense, the food consuming capacity and standing crop of the prey population will decrease. The decrease of prey standing crop associated with a given yield can be minimized by the predator if he chooses his yield in such a way as to maximize population efficiency. This can generally be accomplished by taking yield animals

which are about to die in any case, so that their replacement cost would have to be paid even in the absence of the predator.

APPLICATION OF THE THEORY

First order evaluations of the various concepts of efficiency have been made in laboratory populations of *Daphnia pulex* by Richman (1958), Armstrong (1960) and Slobodkin (1959). All three workers have depended on the caloric determinations of *D. pulex* and *Chlamydomonas reinhardi* made by Richman.

Richman (1958) analyzed the growth and feeding of *Daphnia pulex*.

Slobodkin provided an initial theoretical analysis of laboratory predation experiments (1959) and that analysis has been considerably amplified and modified in the present paper.

Armstrong has reconsidered certain of the theoretical assumptions of both Richman and Slobodkin and has amplified their calculations, in addition to providing new data on growth and predation.

All three workers dealt with a system consisting of *Daphnia pulex* and *Chlamydomonas reinhardi* in which the Daphnia were maintained in conditioned tap water and the algae were grown on sterile agar. Algae was fed to the Daphnia by washing it off the agar, measuring its optical density with a photometer and adding an aliquot of suspension to the Daphnia. Any of the three above cited papers will provide more detailed information on culture techniques.

Richman collected 50 mg. dry samples of Chlamydomonas. These were combined with 250 mg. of benzoic acid and burned in a semi-micro calorimeter bomb. Twelve determinations gave a mean of 5289 cal./gm. on a dry weight basis or 5506 on an ash-free dry weight basis. These figures are very close to those for other Chlorophyceae. The mean of 17 analysis of five species reported by Ketchum and Redfield (1949) is 5340 cal./gm. dry weight and 6154 cal./gm. ash-free dry weight. The caloric content of one Chlamydomonas cell is given by Richman as 1.308×10^{-6} cal.

He sorted *Daphnia pulex* into three size categories. Dried samples of 10-25 mg. were combined with c. 275 mg. of benzoic acid and burned. Mean caloric contents per gram were 4059 ± 203, 4124 ± 229 and 5075 ± 235 respectively for animals of mean length 0.7, 1.3 and 1.8 mm.

Trama found from 5295 to 5975 cal./gm. in the may fly *Stenonema pulchellum* (Trama, 1957). Golley (undated mimeographed sheets) reports cal./gm. determinations for a variety of animals. The extremes are 1780 for the mud crab *Panopius herbsti* and 6223 for *Mus musculus*. Presumably the cal./gm. ash-free dry weight would be somewhat higher since all his reported values for whole Malacostraca seem low, indicating possible inclusion of the mineralized exoskeletons in the samples.

There is sufficiently close agreement between Richman's analyses and the various values reported by Golley and Ketchum and Redfield, to indicate that neither *Daphnia pulex* nor Chlamydomonas are at all extraordinary
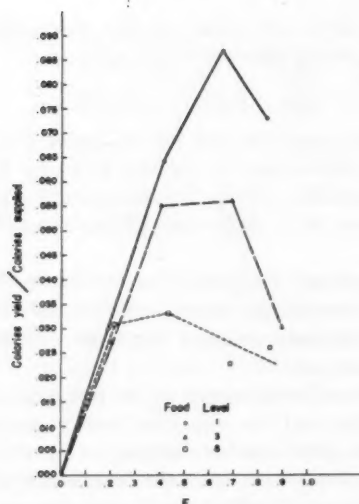
FIGURE 2a. Food chain efficiency on the ordinate vs. F on the abscissa for
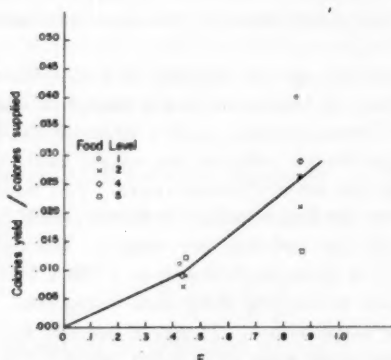populations in which adult animals were preferentially removed as yield.

FIGURE 2b. Identical with 2a except that young animals
were preferentially removed as yield.

in caloric content. This point is of some importance since I will later make
the claim that ecological efficiencies are quite likely as similar as caloric
contents.

Using Richman's caloric content data Slobodkin (1959) assumed three con-
version constants which were used to translate numerical census and yield
data, derived from 22 laboratory populations, into terms of calories. In addi-
tion, the number of Chlamydomonas cells provided for these populations was
estimated and translated into calories by using Richman's value for calories
per algal cell. This provides a direct estimate of I_F.
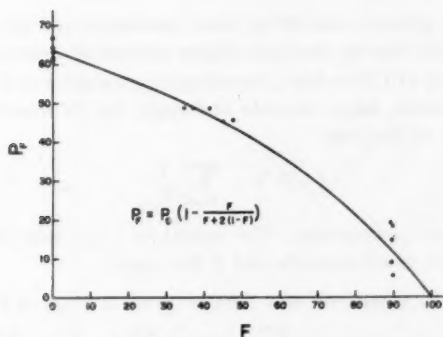
FIGURE 3. P_F, for populations in which young animals were preferentially removed, vs. F.

From I_F and the calories of yield the food chain efficiency could be evaluated directly for each population. This is presented as a function of the intensity of the predation process (figure 2). This measure of fishing intensity is defined elsewhere (Slobodkin, 1957, 1959) and for present purposes we need simply indicate that it is a fishing rate set as a per cent of the births occurring in the population.

Daphnia population standing crops are linearly proportional to their food consumption in the absence of predation (Slobodkin, 1954). There is a simple relation between F and standing crop when all food is consumed, namely

$$(14) \qquad \frac{P_F}{P_O} = \left(1 - \frac{F}{2-F}\right)$$

(Slobodkin, 1957) figure 3. These two relations were assumed generally valid for Daphnia populations and were used to estimate the proportion of the food provided (I_F) that was actually eaten. From this, values of I, the food ingested, could be computed for each population.

Armstrong (1960) computed food ingestion for some of the populations discussed by Slobodkin (1959) on the basis of filtration rate estimates. Comparative values are shown in table 1 and are seen to be of the same order of

TABLE 1

Population	Armstrong (1960)	Slobodkin (1959)	
		I	I'
1.25 A	8.1	8.3	8.6
1.50 A	8.1	7.1	7.9
1.75 A	8.1	8.1	7.7
1.90 A	7.7	6.2	4.9
1.50 Y	8.1	8.1	9.0
1.90 Y	8.0	7.3	9.5

magnitude, but in general somewhat lower estimates of I are derived by the method of Slobodkin than by the more direct method of Armstrong.

Having estimates of I/four days, standing crop calories and also yield/four days of small animals, large animals and eggs, for 22 experimental populations, an equation of the form

$$(15) \qquad I = P'c + \sum \frac{Y_i}{E_{pi}}$$

was set up for each population. The subscript i can take the values A for large animals, S for small animals and E for eggs.

This system of 22 equations was then reduced to a set of four equations:

$$
\begin{aligned}
(16) \quad
&\sum_{1}^{22} P'I = (c) \sum (P')^2 + \frac{\sum P'Y_A}{E_{pA}} + \frac{\sum P'Y_Y}{E_{pY}} + \frac{\sum P'Y_E}{E_{pE}} \\
&\sum Y_A I = (c) \sum Y_A P' + \frac{\sum Y_A^2}{E_{pA}} + \frac{\sum Y_A Y_Y}{E_{pY}} + \frac{\sum Y_A Y_E}{E_{pE}} \\
&\sum Y_Y I = (c) \sum Y_Y P' + \frac{\sum Y_Y Y_A}{E_{pA}} + \frac{\sum Y_Y^2}{E_{pA}} + \frac{\sum Y_Y Y_E}{E_{pE}} \\
&\sum Y_E I = (c) \sum Y_E P' + \frac{\sum Y_E Y_A}{E_{pA}} + \frac{\sum Y_E Y_Y}{E_{pY}} + \frac{\sum Y_E^2}{E_{pE}}
\end{aligned}
$$

This set of equations was then solved for c, and the three E_{pi}.

$c = 1.68$ cal./cal. day, $E_{pA} = .48$, $E_{pY} = .036$, $E_{pE} = .062$.

We have implicitly assumed that the increments in standing crop maintenance cost associated with the various kinds of yield are additive. This assumption probably does not hold at high rates of yield production but precise analysis of the interaction has not yet been made. The E_{pi} are dimensionless, while c has the dimensions $\dfrac{\text{cal.}}{\text{cal.} \times \text{days}}$

The values E_{pi} found from equation (16) are the population efficiencies that would presumably be associated with predation that took only one category of organism as yield. The calculated value of c successfully predicted the mean standing crop of five control populations which did not enter directly into the analysis of equation (15). (Observed 4.8, calculated 4.7). The control populations were used in computing I for each population by means of the relation shown in figure 3.

There also exists a population efficiency for any distribution of the age and size of yield organisms at a steady state in a particular population.

From our previous assumptions and equations (11) and (14) this can be determined for each population, as

$$(17) \qquad E_p = \frac{\dfrac{2Y}{F} - Y}{I}.$$

The only explicit free variables in this equation are Y and F, since I has already been adjusted in value by the use of (14). In addition, the age and
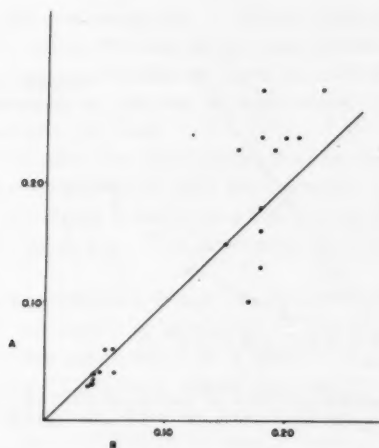
FIGURE 4. The ordinate (A) is given by $E_p = \dfrac{\dfrac{2Y}{F} - Y}{I}$. The abscissa (B)

is $E_p = \sum \dfrac{Y_i / \sum Y_i}{E_{pi}}$; The line assumes $A = B$.

size distribution of the yield are free to vary from population to population, thereby permitting the estimation of E_p from the composition of the yield and the E_{pi} as

(18)
$$\frac{1}{E_p} = \sum \frac{Y_i / \sum Y_i}{E_{pi}}$$

The relation between population efficiency estimated from (17) and from the relative composition of the yield (18) is shown in figure 4.

The I′ values listed in table 1 are the result of substituting c and the E_{pi} from the solution of equation (16) back into equation (15) for each population and solving for the input. The fact that the individual values I′ tend to diverge from Armstrong's estimates more than do the values of I must be attributed to non-linear effects. Ecological efficiency, expressed as $\dfrac{Y}{I'}$ is presented in figure 5 as a maximum estimate of ecological efficiency. The maximum estimate obtained is 12.5 per cent and it seems clear that ecological efficiency would not exceed 14 per cent under any conceivable experimental circumstances.

Values for ecological efficiency of animals in the field, summarized by Patten (1959) include a value of 75 per cent from Teal (1957) which seems almost impossible, a rather high value of 21 per cent (Lindeman, 1942) and eight other non-zero values ranging from 5.5 per cent to 13.3 per cent. There is no significant relation between trophic level and efficiency in these eight values. Top trophic levels have zero ecological efficiency by definition.
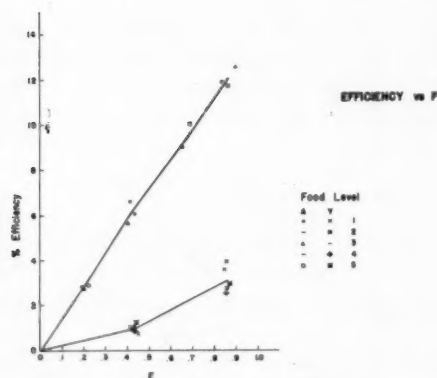
FIGURE 5. A maximum estimate of ecological efficiency in the Daphnia
populations. Ordinate: Y/I'; abscissa: F.

The Daphnia experimental maximum is therefore in good accord with other
data. It seems likely on general grounds that any population in nature will
be producing yield at close to its maximum steady state efficiency.

Combining life table data with growth data Armstrong could compute a
table of E_i for the age categories "eggs," "young," "small," "large" and
"adult." The process of solution was remarkably ingenious but would in-
volve excessive digression to present here. These efficiencies are pre-
sented diagrammatically in figure 6, with the omission of the data for eggs.
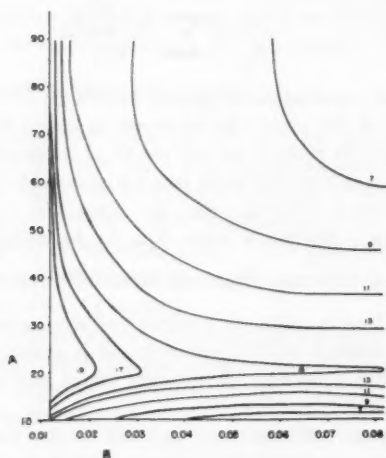
FIGURE 6. Individual growth efficiency × 100 of *Daphnia pulex* as a function of
Chlamydomonas concentration in thousands of cells per ml. (ordinate) and the ca-
loric content of the animals (abscissa). (Using data from Armstrong, 1960).

In excessively low concentrations of algae, growth efficiency is low, since the effort involved in feeding is not compensated adequately by the food acquired. As algal concentrations increase, individual efficiencies increase and then decrease as the rate of ingestion of food exceeds the capacity of the gut to digest the food.

Individual growth efficiencies in Daphnia are somewhat higher in maximum value than ecological efficiencies. They are dependent on the food consumption and growth of individual animals as a function of time and on the energetic cost of producing an egg. (See Armstrong, 1960; Slobodkin, 1959, Appendix B.)

The rather startling difference in age dependence between population efficiency and growth efficiency is explicable in terms of the distribution of life expectancy and food consumption as a function of age. Frank, Boll and Kelly (1957) and Pratt (1943) have shown that Daphnia life expectancy decreases as a function of age, after the first week of life. Various workers (Richman, 1958; Ryther, 1954) have shown the rate of filtration to be considerably greater for an adult Daphnia than for a small Daphnia. Removal of an adult Daphnia will therefore be expected to make relatively little difference in the mean life expectancy of the animals in the population, not only because the adult animals' probability of survival in the absence of predation is not particularly high but also because its removal results in a food increase for the survivors which tends to lengthen their life expectancy. This, in effect, decreases the denominator of equation (11). At the same time the large size of an adult tends to increase the numerator. The older and bigger an animal gets, the greater this effect. To remove animals that are growing slowly, have lived most of their time and have a low reproductive value (see Fisher, 1958) is the epitome of prudent predation and therefore has a high population efficiency. The consumption of old sows will do little to deplete a pig population, while consuming suckling pig in equal quantity will be disastrous, despite the high growth efficiency of the piglet and the low growth efficiency of the sow. This may be verified at any meat market.

CONCLUSIONS

Three types of efficiency have been defined. These are:

1. Ecological efficiency, the steady state ratio of yield to food ingested. This is of primary interest in analysis of natural community interactions. There is some reason to believe that ecological efficiency, at least in aquatic environments, will always have values of from five to 15 per cent.

2. Population efficiency, the steady state ratio of yield to the alteration in population maintenance produced by the removal process. The precise value of population efficiency will depend on the age distribution of the animals removed and the population and growth dynamics of the population in question. It may have values greater than one, under some circumstances. In Daphnia it varies from four per cent for the removal of young animals to

48 per cent for old animals. It is of primary interest in establishing criteria for the removal of yield, by relating efficiency to standing crop size.

3. Growth efficiency, the ratio of the calories in an individual organism to the calories expended in the course of its development. This is dependent on a variety of physiological responses of the organism to its immediate environment and has no direct relation to community dynamics. In Daphnia the extreme values found by Armstrong (1960) are 37 per cent for eggs at 20,000 algal cells per ml. and six per cent for adults at algal concentrations of 70,000 cells per ml.

The Daphnia values for all three types of efficiency may be considered typical, at least until more data are available for other species, since the ecological efficiencies determined from Daphnia seem of the same order as those determined from various natural situations.

SPECULATION

A single laboratory population requires approximately two to five hours of work per week for a year, not counting data reduction time or effort. A significant number of populations must be run in any one experiment.

Field studies are even more time consuming and expensive. The laboratory suffers from a lack of reality and the field from a lack of repeatability. At those points where concepts are comparable, the Daphnia laboratory studies agree with various field studies, enhancing my faith in the applicability of the laboratory and the reliability of the field.

As the phenomena that cry for explanation by the physiologist and biochemist are the simple observational facts of animal life, so the phenomena that must be predictable from any ecological theory are the facts of natural history and species abundance distributions. So far we are a long way from explaining these facts. The hope is raised by the present study that just as the metabolism of all organisms turned out to be essentially the same, so the economy of all populations may turn out to be roughly the same. The only way to tell is to repeat these rather painful studies on as many organisms as possible in the laboratory, if possible with considerable increase in precision. I expect to find that ecological efficiency will have approximately the same maximum throughout the animal kingdom, that growth efficiency will vary as a function of age to the same degree as growth rate and that population efficiency as a function of age will vary somewhat more widely, just as population growth curves are more variable than individual growth curves.

In further field studies, it is more difficult to make clear predictions of the pattern that future data will show. I can, however, make a guess. Sampling errors and errors in the conversion of animals to energy units and errors due to failure to have steady state data will all diminish.

In my own laboratory, Richman and I are getting equipment in operating order which will permit us to measure the calories released on combustion of tissue samples weighing as little as four mg. Golley, in Georgia, is now collecting data on larger animals. In a few years it should be possible to

convert biomass data from field studies directly into energetic units, not only for large animal studies but for studies of terrestrial and aquatic microfauna. I expect that the use of direct conversion constants for each species will considerably increase the precision of field studies of energetics.

Concurrently, the laboratory predation studies are now being repeated on two species of Hydra and on Chlorohydra. I hope that this will test the applicability of the efficiency values determined for Daphnia to carnivorous animals.

The apparent differences between the estimates of food chain efficiency of corresponding trophic levels in different communities will also tend to vanish. I would guess that herbivores in general will have an efficiency of from ten to 13 per cent. Higher trophic levels may quite likely have slightly lower efficiencies. The presently accepted order of magnitude for food chain efficiencies of from c. six to c. 15 per cent is almost certainly correct.

In the absence of yield removal, the corpses in a laboratory Daphnia population represent five per cent of the energy input. Even on high trophic levels, in which predation in the normal sense is not occurring, an efficiency of conversion to decomposer of the same order as the other efficiencies in the system might be expected.

Assuming that we do find constancy of the food chain efficiencies in a steady state community, what type of theoretical structure can be built with this information? By itself, it tells us relatively little that would not have been predictable from elementary thermodynamics or elementary biochemistry. In combination with other ecological information it may provide a set of restrictions that will severely limit the range of possible ecological speculation.

The basic theoretical problem of community ecology is to construct a model or metamodel (Slobodkin, 1958) based on a simple set of assumptions that will generate not only the steady state conditions of the biosphere at a particular instant but the responses of these steady states to various climatic and geologic perturbations. These responses will constitute a theoretical reconstruction of evolution and almost incidentally will be a guide to exploitation of the natural world by man.

It seems possible that the following ecological generalizations are valid.

1. Food chain efficiencies can only have a narrow range of values.

2. Species abundance distribution patterns can only take the form of distributions generated from the theory of interspecific competition (Hairston, 1959; MacArthur, 1957).

3. Pairs of competing species must have a certain minimum of ecological difference if they are to coexist in a steady state (Hutchinson, 1959).

If we now demand that all models of the ecological world that make any pretense to reality must meet all of these conditions simultaneously we will be saved from unbridled speculations and misleading metaphors.

To the degree that these and other generalizations hold we may eventually be able to turn to the mathematician or even to his idiot cousin, the IBM machine, and ask him, or it, to build us all the theoretical models which will

meet our restrictions and still maintain steady states and evolve properly under perturbation. At that time, community and population ecology will enter the company of the exact sciences.

In the interim we must increase the precision of those measurements which we know must be made and test the range of applicability of those generalizations which now seem valid.

SUMMARY

The energetic relation between different trophic levels and populations in a community involves primarily potential energy transfer in complex feedback systems, making the applicability of existing steady state thermodynamic theory questionable, since the requirements for direct evaluation of entropy are not met by ecological systems. The only form of energy considered here was potential energy.

The efficiency of a population does not have a unique meaning. Three different concepts of efficiency were defined and evaluated for *Daphnia pulex*. Two of these, the ecological efficiency and population efficiency, refer to the population level. The growth efficiency refers to individual organisms.

Ecological efficiency is a function of the rate of removal of yield and of the kind of yield animals removed. Population efficiency is a function of the kind of animals removed as yield and the interaction between these animals and the population. Growth efficiency does not depend on the removal of yield at all. It is a function of individual food consumption, growth rate and the energetic cost of reproduction.

These three are interrelated. In general, for a particular system of predation ecological efficiency is proportional to population efficiency. Population efficiency is related to the individual growth efficiency through the effect of the removal of animals on the maintenance cost per calorie of standing crop, which in turn is a function of growth efficiency.

The maximum ecological efficiencies found in the Daphnia experiments are of the same order as ecological efficiencies found in nature, implying that ecological efficiency is effectively constant. Presumably the observed value of c. ten per cent has selective significance.

In speculating on the future development of community ecology, I suggested that certain generalizations now available, including the approximate constancy of ecological efficiency, restrict the development of possible theories. When a sufficient number of these generalizations have been stated and tested a comprehensive predictive general theory of community ecology will appear, if only by the elimination of all conceivable theories whose predictions do not conform to the generalizations.

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I am grateful to the staff and graduate students that have participated in the community ecology seminar at the University of Michigan for their discussion of this work. Drs. Armstrong and Richman have been particularly helpful. Dr. Peter Ovenburg has criticized the mathematical presentation. Profs. G. E. Hutchinson, Anatol Rappoport and Karl Guthe have been liberal with their knowledge and encouragement.

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GLOSSARY OF SYMBOLS

Symbol	Units	Meaning
c	calories/(calories × days)	Maintenance cost of one calorie of standing crop for one unit of time
Δc	calories/(calories × days)	Increment in maintenance cost per calorie of standing crop attributable to the removal of yield.
d_x	animals/animals	The fraction of animals born at time 0 that die during the age interval x.
D_x	animals/days	The number of animals that die during the age interval x.
E	$\dfrac{\text{calories/time}}{\text{calories/time}}$	Yield calories divided by input calories. Ecological efficiency.
E_i	$\dfrac{\text{calories}}{\text{calories}}$	Potential energy in an individual of age i, divided by the potential energy needed to replace that individual. Growth efficiency.
E_p	$\dfrac{\text{calories/time}}{\text{calories/time}}$	Yield calories divided by the difference in maintenance cost between the population producing the yield and a corresponding control population. Population efficiency.
E_{pi}	$\dfrac{\text{calories/time}}{\text{calories/time}}$	Population efficiency for the situation in which the yield consists exclusively of animals age i.
i and j	days	Age categories.
l_x	animals/animals	The fraction of animals born at time 0 that survive to time x.
N_o	animals/days	Number of newborn animals produced in a population during one time interval.
P	calories	Steady state standing crop caloric content of a population.
q_x	animals/animals	The proportion of animals that survive up to an age interval that die during that interval.
S_x	calories	The calories of potential energy contained in an animal of age x.
$\sum$		Summation sign.
x	days	An age category. (Occasionally used as a size category.)
Y	calories/time	Total steady state yield removed from a population per unit time.

GLOSSARY OF SYMBOLS *(continued)*

Symbol	Units	Meaning
Y_i	calories/time	Steady state yield of animals age i removed from a population per unit time.

Note: Except for c' and $\Lambda c'$, in equations (3) and (4), a symbol with a prime (that is, P' or S'_x) refers to a property of a population subject to predation, but is otherwise understood to have the same meaning as the corresponding symbol without the prime (that is, P or S_x).

In the discussion of entropy the symbols all have their conventional meanings.

Symbol	Meaning
ΛF	Change in free energy
ΛH	Change in enthalpy
Q'	Non-entropic heat.
ΛS	Change in entropy.
T	Absolute temperature

BIOCHEMISTRY OF ADAPTATION IN PLANTS TO ENVIRONMENT*†

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Adaptation, or the ability of a plant to "fit" an environment, is dependent upon mainly the flexibility of the biochemical systems of the plant so as to enable it to adjust to the environment. If any one process that controls growth is affected too greatly by the environment so that an essential metabolite or reaction becomes limiting, the plant will not be able to adapt to the environment. Thus, whether or not an organism will be able to adapt to an environment is similar to the problem of whether a mutation will be lethal to the mutant organism. The present discussion will center upon this concept of adaptation; namely, that adaptation to an environment depends upon an organism not having a deficiency of an essential enzyme or metabolite induced or made apparent by the environment. Various experimental evidences in support of this concept will be presented for lower and higher forms of plants. This subject has been reviewed previously, in part, by Bonner (1957) and Kurtz (1958).

CHEMICAL CONTROL IN LOWER FORMS

The most clearcut examples of the chemical basis of climatic diseases are to be drawn from the work of H. K. Mitchell and his co-workers on temperature-sensitive mutants of the red-bread mold, *Neurospora crassa*. Temperature-sensitive mutants are phenotypically normal at one temperature, but are phenotypically mutant at another, usually higher, temperature. Thus a mutant was found that grows normally up to $25°C$, but above this temperature there is a rapid decrease in growth until, at $28°C$, no growth occurs (figure 1). High temperatures apparently limit growth of the mutant by controlling some essential reaction, because only 2.5×10^{-4} grams/liter of the B-vitamin riboflavin restores growth of the mutant at temperatures that are inhibitory otherwise. Thus adaptation of the mutant to temperatures above $28°C$ is limited by a deficiency of an essential metabolite. A number of other temperature-sensitive mutants of Neurospora and their chemical cure have also been described (Horowitz, 1950).

It is not known how an essential metabolite becomes limiting at high temperatures in temperature-sensitive mutants of Neurospora: gene action may be limited; the essential metabolite may be thermolabile; the enzyme that catalyzes the formation of the essential metabolite may be thermolabile or its activity reduced; the essential metabolite may be frittered away by an
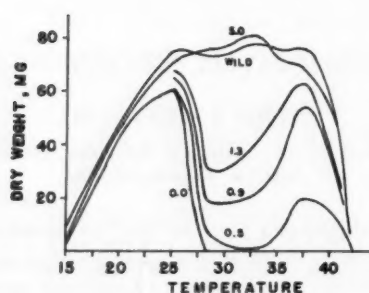
FIGURE 1. Growth (mg. dry weight) of the wild type and temperature-sensitive mutant of *N. crassa* at different temperatures and riboflavin concentrations (μg./20 ml. of culture). Redrawn from Mitchell and Houlahan (1946).

enzyme whose activity is increased. Although these or other mechanisms may be operative, there is some evidence that differential thermolability of enzymes determines adaptability of a mutant. Thus, Horowitz and Fling (1953) found that the tyrosinase of thermostable strains of Neurospora is more thermostable than the tyrosinase of thermolabile strains (table 1). As will be shown later, thermostability of enzymes is apparently the secret of thermophily in microorganisms.

A study of *N. crassa* by Hirsch (1954) concerning temperature-dependent production of cellulase has interesting ecological implications. Hirsch found that cellulase is produced at 35°C but not at 25°C. *N. crassa* is a tropical or subtropical mold that grows on burned trees, and "... it seems possible that the ability of certain strains to elaborate cellulase at higher temperature ranges is a determining factor in their ability to occur in the wild state in the warmer climates but not in the temperate or cold ones (apart from bakeries, etc.) and thus a direct enzymological explanation can, perhaps, be given for the occurrence of the organism in its own particular ecological niche, be this on a strain or species level (1954)."

The chemical basis of high temperature lesions of certain temperature-sensitive mutants of bacteria has been found, but of greatest interest is a study of the thermolability of an enzyme of one of these mutants. Maas and Davis (1952) found, as did Horowitz and Fling for Neurospora, that an es-

TABLE 1

Thermostability of tyrosinase from thermostable (T^s) and thermolabile (T^1) strains (Horowitz and Fling, 1953)

Temperature °C	Half-life of tyrosinase at each temperature, in hours	
	T^s	T^1
25	29	16.5
35	15.5	5.5
59	0.5	0.05

sential enzyme (pantothenate-synthesizing enzyme) in the temperature-sensitive mutant is thermolabile; thus the requirement at higher temperatures for the metabolic product of this enzyme (table 2). Of particular importance is the observation that the thermostabile protein from the wild type does not stabilize the thermolabile protein from the temperature-sensitive mutant.

TABLE 2

Heat inactivation of purified extracts of the pantothenate-synthesizing enzyme of *Escherichia coli*. Data from Maas and Davis (1952)

Source of extract		Length of exposure at 35°C.		
Wild type	Temp.-sens. mutant	0 min.	30 min.	60 min.
		Residual	Enzyme	Activity
+	−	100	86	98
−	+	100	15	3
+	+	100	50	48

A large body of evidence has been gathered by Koffler (1957) and Koffler et al. (1957) in support of the hypothesis that thermostability of essential protoplasmic proteins is the factor limiting growth of organisms at above-normal temperatures. On the basis of changes of the physical properties of purified proteins from bacterial flagella, Koffler et al. have concluded that thermophilic bacteria are able to survive at high temperatures because their protoplasmic proteins have a configuration that stabilizes them against degradation by heat. Along this same line, Campbell (1954) showed that amylase isolated from a facultative thermophilic bacterium grown at 55° was much more heat-stable than a similar preparation from cultures grown at 35°C. The implications of this finding are most interesting.

CHEMICAL CONTROL IN HIGHER PLANTS

Turning now to higher plants, the earliest demonstration of the chemical control of a temperature disease was by Bonner in 1943. In this case restricted growth of Cosmos plants at a low (20°C) temperature was partly cured by the addition of the B-vitamin thiamine to the nutrient medium in which the Cosmos were growing.

More recently Langridge and Griffing (1959) have studied elegantly several high temperature lesions of *Arabidopsis thaliana*. High temperature damage of two temperature-sensitive races was partly cured with biotin, and temperature damage to a third race was partly cured with yeast extract, nucleic acids, or cytidine.

Thus far the discussion has been concerned mainly with adaptation to temperature. Some insight into the chemical basis of drought resistance is also apparent from the work of Kessler (1959b) who found that the application of adenine to bean plants and peach and grape leaves increased toler-

ance to drought. The tolerance was greatest when adenine was applied to germinating seeds and seedlings and very young leaves.

Adenine was shown by Highkin (1957) to be also involved in heat resistance of peas. A heat-susceptible variety of peas contains equal amounts of adenine at both low (14°C) and high (26°C) temperatures, whereas in a resistant variety the amount of adenine doubles at 26°C as compared with that of plants grown at 14°C. Adenine may be needed to sustain nucleic acid synthesis at high temperatures and water stress, for Kessler (1959b) and Gates and Bonner (1959) observed decreased net synthesis of nucleic acids under such conditions. ···

The chemical control of plant growth has also been investigated in regard to flowering of biennial plants. A biennial plant must receive a cold treatment at the end of the first year's growth in order to induce flowering in the second year. Lang (1956) found that gibberellic acid will stimulate a biennial plant to flower even though it has not received a cold treatment. Whether gibberellic acid is itself formed in biennial plants is not known.

OTHER AREAS WHERE A BIOCHEMICAL CONTROL IS INDICATED
AND FUTURE WORK IS NEEDED

The foregoing examples of the chemical basis of plant adaptation constitute the majority of those known. However, there are several areas of research where a chemical basis is indicated. These will be discussed briefly as suggestions for much-needed future work.

1. *pH requirement.* It is well-known that organisms have rather specific pH requirements of the external medium, but the precise need for these requirements is not understood. As an example of how this problem might be approached, Stokes et al. (1943) found that a mutant of *Neurospora sitophila* requiring pyridoxine in the nutrient medium did so only when the pH of the medium was less than 5.8; above pH 5.8 the pyridoxineless-mutant did not require pyridoxine. Thus the deleterious effect of pH on a plant might be overcome by supplying some essential metabolite.

2. *Osmotic effects.* Osmotic and salinity problems have plagued physiologists for many years. An interesting temperature-osmotic relationship has been uncovered by Langridge (1958). A single recessive mutant of *Arabidopsis thaliana* was found which, at 23°C, had distorted growth, narrow leaves, poor secondary root development, and complete sterility. At 28°C the mutant showed normal growth. Abnormal growth of the mutant at 23°C was shown to be a result of an abnormally low cellular osmotic pressure because the addition of sufficient glucose, sucrose, or potassium sulfate to the medium to raise the osmotic pressure to 2.5 atm. or more, restored normal growth of the mutant. Indeed, by reducing the internal osmotic pressure of a normal plant, growth of the plant resembled the growth of the mutant.

3. *Growth of plants under controlled conditions.* Went (1957) has described some of the numerous effects of controlled environment on plant growth. These effects are too numerous to mention here, but a survey of

them suggests many possibilities for exploring the chemical basis of adaptation: adaptation to various lengths of diurnal cycle, requirements for nyctotemperatures, photoperiodic effects on growth, and sex expression are but a few examples. Went (1958) has already discussed some of these and other physiological adaptations.

4. *Physiological differences of ecological races.* The experimental studies of Clausen, Keck, Hiesey, and their co-workers are well-known. This laboratory is now undertaking the problem of determining physiological differences of races, and preliminary work suggests that races of Mimulus may be described on the basis of different photosynthetic activity (Annual Report, 1957-58).

5. *Mineral nutrition.* The roles of the macro and micro elements in plant nutrition are becoming better understood, and it is possible to envisage the chemical basis of nutrient tolerances and requirements. For example, Kessler (1959a) has shown that zinc regulates ribonuclease activity in fruit trees. Thus zinc controls the metabolism of ribonucleic acids and proteins.

6. *Temperature-induced variability.* If a pea plant is grown for several generations at a constant low (10°C) temperature it becomes dwarfed. But most interesting is the fact that upon returning the plant to optimum growing conditions the dwarfism is perpetuated (Highkin, 1958). This temperature-induced variability persists for only a few generations and the plant gradually returns to normal. No explanation of this phenomenon has been made, but the chemical aspects of it appear most intriguing.

7. *Seed germination.* Certain aspects of seed longevity, viability, and dormancy should lend themselves to the experimental approach used to determine the chemical basis of plant responses to environment.

8. *Arid lands problems.* As might be expected, my interest in the chemical basis of plant adaptation stems from an interest in the adaptation and adjustment of plants to the many stresses typical of arid lands. For instance, MacDougal and Working (1921) showed that stem joints of young Opuntia cactus plants grow at an air temperature of 58°C. In our own work
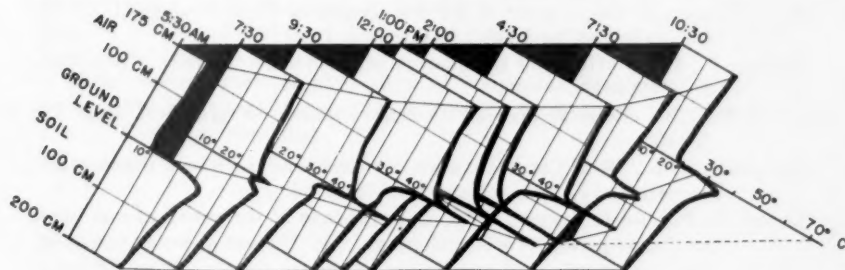

FIGURE 2. Soil and air temperatures at Tucson, Arizona, on 21 June 1915, from 5:30 A.M. to 10:30 P.M. Three lines connect the temperatures during the day at ground level, at 175 cm. in the air above ground level, and at 200 cm. below ground level. From Kurtz (1958), based upon the data of J. G. Sinclair, 1922, Monthly Weather Rev. 50: 142.

(Alcorn and Kurtz, 1959) on saguaro (*Carnegiea gigantea*) cactus seeds we found that no germination occurs at constant temperatures above 30°C. However, dry saguaro seeds may be heated at 83°C for seven days before all viability is lost (Kurtz, 1958). Such heat resistance in the dry state is essential for the survival of the cactus, because the seeds must be able to tolerate extremely high temperatures at the soil-air interface (figure 2). The physiological adaptations necessary for survival in arid lands are many, and a knowledge of the chemical mechanisms of adaptation of native plants should be of great aid for "adapting" economic plants for arid land agriculture.

SUMMARY

It was suggested that the ability of a plant to adjust or adapt to an environment depends upon the organism not having a deficiency of some essential enzyme or metabolite at the new environment. In support of this concept is the finding that decreased growth or death of lower and higher plants at elevated temperatures may be prevented by supplying the plants with certain specific metabolites. The mechanism by which temperature controls the formation of an enzyme or metabolite is not known, but work with proteins from thermophilic organisms points to thermostability of proteins as of prime importance.

There is also some evidence in support of the proposed concept of chemical adaptation as applied to environmental factors other than temperature. Thus certain pH effects, osmotic requirements, physiological differences of ecological races, mineral nutrient requirements, temperature-induced variability, seed germination requirements, and certain arid lands problems may all have a similar chemical basis.

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ECOTYPES AND COMMUNITY FUNCTION*†

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INTRODUCTION

Three statements can be given concerning the ecotype and community function. The first: "The role of the ecotype in community function is primarily one of allowing vegetation to adjust to its habitat." The second: "The simultaneous selection of ecotypic variants within different kinds of plants occupying a common area results in the harmony of a particular stand of vegetation, the community, and its habitat." The third: "The selection of eco-genetic gradients within a number of species results in the continuity of a kind of vegetation, the community-type, over habitat diversity."

Within these three introductory statements, ecotype, ecotypic variation, and eco-genetic gradient refer to genetically-determined variation that is habitat-correlated. Following sampling in habitat extremes genetic differences are usually recognized: edaphic ecotypes, climatic ecotypes, topographic ecotypes, etc. A pattern of ecotypic variation often emerges from sampling in habitats of varying degrees of difference. An eco-genetic gradient often results from sampling through a habitat gradient. Variation observed in the field and possibly habitat-correlated is ecodemal until experimentally substantiated (Gregor, 1944, 1946).

In these statements, the concept *community* is applied to one or more populations in a common spatial arrangement, and the concept *population* is applied to the one or more individuals of a close genetic lineage in a common spatial arrangement. Therefore, there are many kinds of communities, as there are many kinds of populations. The lumping or sorting of certain communities into a particular kind, on any of a number of criteria, results in the recognition of a community-type. Mainly under discussion will be the community-type based on the geographic repetition of a certain combination of species and genera.

In the following discussion, an evaluation of the evidence supporting each statement will be presented. The validity of the first statement concerning the role of the ecotype in community function lies in the demonstration of ecotypic variation and of its correlation with the conditions of the habitat. The second statement concerning the simultaneous selection of ecotypic variants within different kinds of organisms in a given area applies

to the harmony between a local community and its habitat.   The investiga-
tion of the genetic potential of the various community members and the be-
havioral patterns under different site potentials would aid in this analysis.
The uniqueness of a local community can be determined by a comparison
with other communities of the same community-type.   The third statement
concerning the selection of eco-genetic gradients within a number of spe-
cies is applied to the geographic repetition of a combination of certain spe-
cies and genera.   The analysis of ecotypic variation within a series of
species critical to the recognition of such a community-type, and the com-
parative analysis of the members of a number of communities would support
this statement.

<center>ECOTYPIC VARIATION</center>

  Natural selection commonly results in a pattern of ecotypic variation
within a plant species.   In validation of the first statement is the general
occurrence of ecotypes among trees (Pinus, Langlet, 1943; Stoeckeler and
Rudolf, 1956; Kramer, 1957; Acer, Kriebel, 1957; Vaartaja, 1959; Thuja,
Habeck, 1958; Vaartaja, 1959; Pseudotsuga, Morris, et al., 1957; Irgens-
Moller, 1957; Tsuga, Olson, et al., 1959; Vaartaja, 1959; Fraxinus, Wright,
1944a, 1944b; Vaartaja, 1959; Meuli and Shirley, 1937; Betula, Larix, Pi-
cea, Ulmus, Vaartaja, 1959; Populus, Pauley and Perry, 1954), among shrubs
(Artemisia, Ward, 1953; Clausen, et al., 1940; Atriplex, Turesson, 1922,
1925; current studies in Prosopis, McMillan, unpubl.), among grasses (Boute-
loua, Olmsted, 1944; Riegel, 1940; McMillan, 1959; Andropogon, Larsen,
1947; Cornelius, 1947; McMillan, 1959; Poa, Hiesey, 1953a; Deschampsia,
Lawrence, 1945; Panicum, Nielsen, 1944, 1947; McMillan and Weiler, 1959;
McMillan, 1959; Sporobolus, Sorghastrum, Elymus, Koeleria, McMillan, 1959;
Festuca, Bradshaw and Snaydon, 1959), among herbs (Achillea, Potentilla,
Clausen, et al., 1940, 1948; Hiesey, 1953b; Viola, Clausen, 1922, 1926;
Geranium, Böcher, 1947; Plantago, Gregor, 1939; Solidago, Goodwin, 1944;
Armeria, Baker, 1949, 1953; Helianthus, Heiser, 1954; Eupatorium, Kucera,
1958; Streptanthus, Gilia, Kruckeberg, 1951), to cite a partial list.   Among
animal species, the demonstration of ecotypic variation is less general, but
examples are found among insects (Drosophila, Dobzhansky, 1948; Lyman-
tria, Goldschmidt, 1934; Colias, Hovanitz, 1945), among amphibians (Rana,
Moore, 1944, 1947, 1949), among fishes (Gasterosteus, Heuts, 1947, 1949),
and among rodents (Peromyscus, Dice, 1933).

  The above examples have been empirically determined and correlated with
the habitat. In many instances the genetics of the ecological races has been
studied extensively and was the subject of a recent review by Clausen and
Hiesey (1958).   The habitat correlations have been various: light period se-
quence, temperature period sequence, soil moisture, length of growing sea-
son, among others.   In 15 species out of 17 in eight of nine tree genera
(Acer, Betula, Fraxinus, Larix, Picea, Pinus, Pseudotsuga, and Ulmus),
Vaartaja (1959) showed photoperiod ecotypes were correlated with the lati-
tude of seed origin.   These genera, in addition to Populus, in which Pauley

and Perry demonstrated photoperiod ecotypes, represent the most widespread trees north of the tropics. In *Pseudotsuga taxifolia*, Morris, et al. (1957) found early bud-bursting by trees from localities having warm spring days and nights, as in wide valleys. Those with intermediate bursting buds came from higher elevations, with cold spring days and nights. Trees with latest bursting buds came from narrow valleys where cold air drainage resulted in warm spring days and cold spring nights. The characteristic bud bursting was maintained over a period of 22 years at three altitudinal plantations. Among 43 sources of *Acer saccharum*, Kriebel (1957) showed terminal dormancy was correlated with latitude. Stoeckeler and Rudolf (1956) showed growth patterns correlated with latitudinal origin among 29 sources of *Pinus banksiana*. Habeck (1958) demonstrated ecotypic differences in *Thuja occidentalis* in Wisconsin. Those from lowland swamps had growth patterns different from the upland type when grown in the same habitat. Goodwin showed a flowering gradient in *Solidago sempervirens*. Clones from Massachusetts flowered sooner in Rochester, New York, than those from Maryland or Florida. The later flowering of more southerly clones was correlated with the longer growing season toward the south. McMillan (1959) has demonstrated early maturing types from northerly latitudes and high altitudes in Bouteloua, Andropogon, Panicum, Sorghastrum, and Sporobolus. In seven species within these five grass genera, clones of later maturity were from areas with longer growing seasons. In Achillea, Hiesey (1953 b) demonstrated that the race from the northern California coast was able to flower under cool day and night conditions. The race from the Great Valley of California flowered under high day and night temperatures. This flowering response under controlled temperatures was correlated with the temperatures of their native habitats during their usual flowering period. In species of several genera (Silene, Plantago, Armeria, etc.) the maritime populations have been later in flowering and more prostrate than the inland form. While this list includes only a few examples, it indicates the general occurrence of habitat-correlated variation in plants.

The general occurrence of ecotypic variation within plant species strongly supports the view that ecotypes play a significant role in vegetational adaptation. There have been few instances in which ecotypic variation has not been demonstrated within a widespread plant species. This could result from a hesitance to publish what is generally considered to be the normal. However, since ecotypic variation is becoming the expected mechanism for wide plant distribution, perhaps non-variable species will gain more attention. Of 11 grass species studied in Mid-America by McMillan (1957, 1959), only Stipa showed a lack of habitat-correlated variation. In three species, *Stipa spartea*, *S. comata*, and *S. leucotricha*, behavioral characteristics were very similar within a species for clones from widely separated and extremely different habitats. In local populations of Stipa, the observed differences within the species, result chiefly from the local habitat sequence in that particular year.

COMMUNITY ADAPTATION

The evidence for evaluating the second statement, concerning community adaptation, and the third, concerning the continuity of a community-type, will be drawn largely from studies of the grasslands of Mid-America. This is necessitated by the scarcity of studies dealing with the role of the ecotype in community function, resulting, in part, from the emphasis of the taxonomist upon studies of ecotypic variation, and from the associated lack of emphasis by the ecologist. However, the original studies of Turesson (1922, 1925) in genecology are particularly noteworthy owing to their ecological viewpoint. In these transplant studies, Turesson demonstrated characteristics common to many maritime ecotypes within a number of herbaceous species in Sweden. His comparison with ecotypes of the same species from inland habitats formed a sound basis for the ecological evaluation of communities. The later transplant studies of Clausen, Keck, and Hiesey (1940) dealt with herbaceous species from forested areas in California. Alpine ecotypes in a number of species were differentiated from sub-montane ecotypes and these in turn from foothill and coastal ecotypes. Their studies in Achillea (1948), involving more frequent sampling along an altitudinal gradient in the Sierra Nevada, suggests that eco-genetic gradients may exist in many of the species studied earlier.

An ecological objection to the studies of both Turesson and of Clausen, Keck, and Hiesey is that there was no evaluation of the ecological dominants, that is, the most conspicuous plants, trees, in a forested area. Although both give evidence of the simultaneous selection of ecotypes within a number of herbaeeous species in a common habitat, ecologists have relegated these studies to taxonomy. Ecologists have considered alpine communities distinct from sub-alpine communities and these distinct from lower altitudinal communities, because of the different assemblages of ecological dominants involved. The occurrence of a gradient of ecotypes within herbaceous species does not alter the observed zonation of forest types in the Sierra Nevada.

The grassland vegetation offers a superb object of study for determining the relationship of ecotypes to community function. Here, the ecological dominants, the grasses, are well suited to an ecotypic analysis. Here, also, the combination of certain species and genera remains fairly constant over an obviously variable habitat. It was reasoned, therefore, that studies of ecotypic variation in grasslands might be focused effectively upon a better understanding of the community and of the distribution of a particular community-type. The earlier studies of workers in the Soil Conservation Service, agronomists, and other ecologists in demonstrating behavioral variation within the common grass species were instrumental in directing the future course of these studies. For example, the studies of Olmsted (1944) and his students presented evidence in *Bouteloua curtipendula* of ecotypes differing in response to length of light period, the northern forms flowering under longer light periods and the southern forms under shorter light periods.

The studies of Cornelius (1947) and of Larsen (1947) in *Andropogon sco-parius* demonstrated behavioral patterns attuned to shorter growing seasons by northern forms and to longer growing seasons by more southerly forms.

In the grassland investigations to be evaluated here, the focus has been upon (a) the behavior of individual plants, (b) the comparison of behavior patterns within a population, and (c) the comparison of behavior patterns in a number of populations within the same community. The studies have included an analysis of behavior patterns under natural habitat conditions as well as a number of experimental habitats including transplant gardens in Lincoln, Nebraska, and Austin, Texas, and controlled greenhouse conditions.

In six grass species in Nebraska, McMillan (1957) showed that populations from a southeastern community began flowering two weeks later than populations from a sandhill community of central Nebraska. Populations of both communities showed behavioral differences when compared in the loess soils at Lincoln and in the sandy soils near Halsey. When grown in the sandhills, all of the populations were approximately two weeks later in flowering than when grown 200 miles further east in Lincoln at a similar latitude. This basic study has been expanded to include grassland communities from southern Saskatchewan and Manitoba to southern Texas.

From a community in the vicinity of Watertown, South Dakota, clones of seven populations were studied in the transplant garden (McMillan, 1959): *Bouteloua gracilis, Bouteloua curtipendula, Andropogon scoparius, Panicum virgatum, Sporobolus heterolepis, Andropogon gerardi,* and *Sorghastrum nutans.* During 1958 at Lincoln, Nebraska, all of the clones flowered prior to July 18. From a community near Manhattan, Kansas, clones of populations representing the same seven species had initial flowering at Lincoln after July 18 (figure 1). Initial flowering in the Kansas clones extended into mid-September. In an eighth population (*Stipa spartea*) from South Dakota and from Kansas, similar behavior was shown. In a ninth population (*Elymus canadensis*), the earliest flowering was in the clones from the southernmost community. In reducing the communities to symbolic form, with the prime indicating early maturity, they could be represented as follows: Watertown, South Dakota, a, b, c′, d′, e′, f′, g′, h′, i′, and Manhattan, Kansas, a, b′, c, d, e, f, g, h, i. Each community is unique, though the same combination of species is represented. Each is in harmony with its habitat through the selection of ecotypic variants in eight of the nine species studied. Included within those nine species were those characterizing the true prairie type of community of Clements (1936), and representing five of the six community-types used by Weaver (1954) in his analysis of the true prairie.

The members of two communities, one at Fertile, Minnesota, and one near Colorado Springs, Colorado, at 2200 m. elevation, had similar behavior patterns in the transplant garden (McMillan, 1959). Population samples of the same six species reached initial flowering over the same 40-day span in Nebraska. When compared under controlled conditions, involving 12½-, 14-

No. of Days

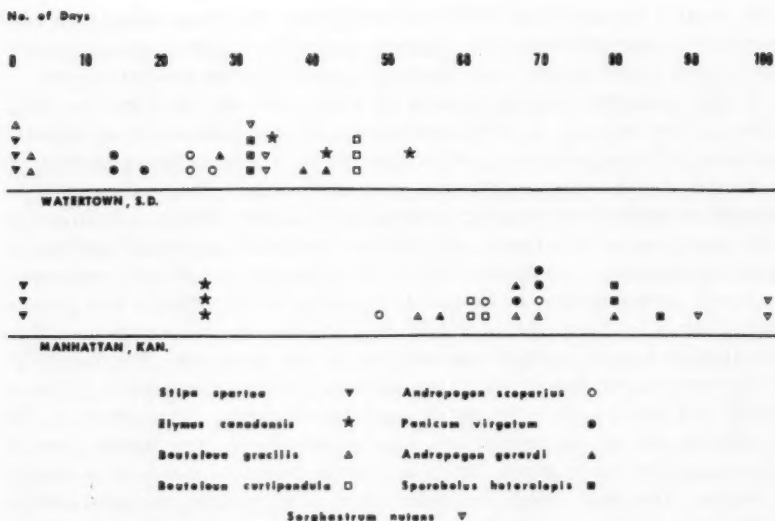0   10   20   30   40   50   60   70   80   90   100

FIGURE 1. Responses in a Lincoln, Nebraska, transplant garden. Symbol for each clone indicates the number of days after June 1, 1958, that initial anthesis occurred. For *Stipa spartea*, a late stage of inflorescence development is designated, anthesis being rarely observed. Two clones of Elymus are from a community directly north of Watertown.

and 15½-hour light periods, flowering differences were shown. In *Bouteloua gracilis*, a broader range of tolerance to length of light periods was shown by clones from the Colorado community than by clones from Minnesota which flowered only under the longest light period. In *Panicum virgatum*, both populations responded similarly to 14- and 15½-hour light periods, but differed under shorter periods. The Minnesota clones of Panicum went dormant after a short growth period under 12½-hour light periods, while the Colorado clones grew normally under the same light period but failed to flower.

The community studies support the statement that the simultaneous selection of ecotypic variants within a number of species accounts for the harmony of a given community and its habitat. Natural selection in favoring responses attuned to recurrent habitat sequences has produced vegetational site-climaxes composed of ecotypic variants.

CONTINUITY OF A COMMUNITY-TYPE

In the investigation of a community-type over a diverse series of habitats, the role of ecotypic variation was studied in the distribution of the characteristic species. In nine grass species of central North America, the wide distribution was shown to result from ecotypic variation (McMillan, 1959). In eight species, *Koeleria cristata, Bouteloua gracilis, Bouteloua curtipendula, Andropogon scoparius, Andropogon gerardi, Panicum virgatum, Sorghastrum nutans,* and *Sporobolus heterolepis,* early maturing types have

been selected in northern and high altitude communities. Progressively later maturing types have resulted from the selective pressures of longer growing seasons toward the southeast and at lower elevations. In one (*Elymus canadensis*), early maturity types were from southern communities. In another (*Stipa spartea*), as mentioned above, no behavioral differences characterized the transplanted clones.

A comparison of transplanted clones (McMillan, 1959) indicated the latitudinal and altitudinal trends in community behavior. The community members from Devils Lake, North Dakota, had initial flowering during a span of approximately 40 days. Members of a southern community, Ponca City, Oklahoma, had initial flowering over a period two and one-half to three times longer. The two communities from intermediate localities, Sioux Falls, South Dakota, and Manhattan, Kansas, showed initial flowering over periods of intermediate length. A similar span of initial flowering dates for communities from three western sites and the Devils Lake site was shown. The comparison involved western sites at progressively higher elevations toward the south, Miles City, Montana (715 m.), Wheatland, Wyoming (1480 m.), and Peyton, Colorado (near Colorado Springs at 2200 m.). Communities along an altitudinal gradient from Peyton, Colorado, to Flagler, Colorado (1500 m.) to Hoxie, Kansas (825 m.) and to Manhattan, Kansas (310 m.) showed a gradient with an increasing span of initial flowering dates toward the lower elevations. In a further comparison of four communities, Fertile, Minnesota, Lincoln, Nebraska, Ponca City, Oklahoma, and Peyton, Colorado, under two different light periods, the essential maturity differences shown in the transplant garden were repeated.

When the communities representing the grassland community-type were transplanted from Nebraska to Texas and studied in the Austin transplant garden during 1959 (McMillan, unpubl.), growth resumption was during late February and early March. At Lincoln, Nebraska, growth resumption by the same clones occurred in late April of 1957 and 1958. The earlier date for growth resumption in Texas yielded actively growing plants under shorter light periods than had been present at a comparable stage of growth in the Nebraska transplant garden. The resulting behavior patterns were partially predicted on the basis of daylength studies, but partially unpredicted because of the previously uninvestigated exposure to a long sequence of increasing daylengths and to sustained high day and high night temperatures. In *Bouteloua gracilis*, clones from the southern communities, capable of flowering under short light periods, flowered earliest. The northern clones, having the earliest maturity patterns under the light-period sequence in the Nebraska transplant garden, were the latest to flower in the Texas garden. The northern clones were unable to flower under the short light periods during the early part of the growing period in central Texas. Dormant pieces of North Dakota clones transplanted from Nebraska to Texas in April flowered at the same time as pieces of the same clones that had been actively growing in Texas since late February. In contrast, dormant pieces of Oklahoma clones transplanted in April flowered later than the pieces of the same

clones, which had resumed growth in February. In this material transplanted in April, the flowering pattern in Texas, the Oklahoma clones being later than North Dakota clones, essentially duplicated the response of these clones in the Nebraska garden. In *Andropogon gerardi*, after a short period of growth in Texas, clones from the more northern communities, entered a dormant stage. Similar behavior had been demonstrated under the shortest light periods in greenhouse studies. After a period of dormancy, as demonstrated in the greenhouse, the clones resumed growth. Following this second growth resumption, the northern clones flowered earliest in Texas, even though the stem height of the earliest flowering culms was mostly under 15-20 cm. Clones from northern communities flowered principally in June and early July; clones from Oklahoma and Texas, in July, August and September. The Texas coast clones flowered latest, in mid-September. In *Bouteloua gracilis* and *Andropogon gerardi* a height gradient was demonstrated in the Texas garden during 1959. The northern clones produced the shortest flowering culms, the mid-latitudinal and high altitude clones produced intermediate-flowering culms, and the clones from Texas produced the tallest culms. In *Panicum virgatum* clones from more northerly locations tended to flower earliest, although much variation occurred among individuals of a population. Certain interpopulational differences were shown that had not been observed in the more northern transplant garden, for example, clones from different populations in Iowa were extremely different in height and behavior. Such differences among the Iowa populations were scarcely observed at the Nebraska transplant garden. Flowering of most Panicum clones from Kansas northward was during May and June. Flowering of Oklahoma and Texas clones extended from July for many Oklahoma and Texas panhandle clones to mid-September for coastal clones. In *Andropogon scoparius* flowering of certain northern clones was in June. In certain of these earliest-flowering clones from North Dakota and South Dakota, the inflorescences barely exceeded the length of the leaves, although later-flowering culms were much longer. Flowering among Texas clones extended into mid-October for coastal types.

These studies support the third statement that the continuity of the grassland community-type over much of Mid-America results from the simultaneous selection of eco-genetic gradients in a number of dominant species. The abstraction of discrete communities into a community-type, such as true prairie, mixed prairie, and coastal prairie, is a convenient method for discussing communities with a particular combination of species. Extreme caution, however, should be exercised in generalizing about the characteristics other than distributional for a community-type.

Although community examples are restricted to the grassland vegetation, natural selection operating within forest and scrub communities has resulted in harmony through variation patterns within many of the component species. The demonstrations of ecotypic variation within some of the commonest tree species of North America indicates the significant role of the ecotype in the widespread distribution of a particular kind of forest. Likewise, the

demonstration of ecotypic variation in sagebrush (Ward, 1953) indicates that the broad distribution of our western scrub communities may result from the simultaneous selection of eco-genetic gradients within the characteristic species. The continued investigation of the role of the ecotype in community function should prove a profitable ecological pursuit.

SUMMARY

The result of natural selection is commonly a pattern of ecotypic variation within a species. This has proven to be of rather general occurrence among trees, shrubs, grasses, and herbs, annual and perennial. Among animal species, the demonstration is less general, but includes examples among insects, fishes, amphibians, and rodents. The simultaneous selection of ecotypic variants within different kinds of organisms occupying a common habitat results in unique site-communities. As demonstrated within the grassland type of community, individuals within a number of species have been selected for early maturity at a given site. In another situation, individuals of the same species are of later maturity. The role of the ecotype in community function clearly becomes one of allowing vegetational adjustment to habitat diversity. Genetic gradients within a number of species provide the key to the continuity of a vegetational type over habitat gradients.

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